FACTORS AFFECTING CARABID (COLEOPTERA: CARABIDAE) ASSEMBLAGES IN SUCCESSIONAL SUB BOREAL SPRUCE FORESTS, WITH SPECIAL REFERENCE TO THEIR INTERACTION WITH ANTS (HYMENOPTERA: FORMICIDAE).

by

Duncan Andrew M^{c}Coll

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Abstract

Carabid (Coleoptera: Carabidae) assemblages in west central British Columbia are relatively poorly examined. Additionally, the influence of ants (Hymenoptera: Formicidae) on carabid assemblages is infrequently acknowledged as a factor that affects carabid diversity, distribution, and activity.

The purpose of this study was to examine carabid assemblages in successional sub boreal spruce forests in west central British Columbia, and specifically how they are affected by two species of ants; *Formica aserva* (Forel) and *Camponotus herculeanus* (L). Data pertaining to carabid and ant activity-abundance were collected over a chronosequence of successional forest stages by pitfall trapping. The data were analyzed for the effects of canopy cover, vegetation, and ant influence on carabid species assemblages. Carabids were shown to be influenced by the presence of ants on the basis of a pattern of avoidance, and the frequency of carabid injuries were significantly related to *F. aserva* activity-abundance. An experiment where *F. aserva* nests were introduced into a clearcut was conducted to further examine this relationship confirmed that carabid activity-abundance is affected by ant presence.

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Chapter 1: Introduction

Throughout forested regions of Canada, forestry is a dominant economic, social, political and ecological force. It accounted for $36.3 billon in gross domestic product in 2006, and the alteration through harvesting of 903,009ha of land in 2005 (Canadian Forest Service 2007). Numerous ecological effects initiated by harvesting persist for long periods of time as the stand recovers, and influence the trajectory of stand recovery. Landscape-level alteration of the distribution, shape, species composition, size and juxtaposition of clearcuts on the landscape will likely persist for several stand rotations (DeLong 2002). Within-stand changes initiated by harvesting can affect coarse woody debris (CWD) cycles, as well as distribution, quantity and quality of CWD immediately following harvest (Lloyd 2003), and these effects may persist for many years (Densmore *et al.* 2004). In addition, there may be changes in soil properties through mechanical disturbance (exposure of mineral soil, compaction *etc.*) associated with harvest (Ballard 2000, Page-Dumroese *et al.* 2005), chemical changes associated with altered soil biota (Ballard 2000), and shifts in forest hydrology (Moore and Wondzell 2005). Many of these effects impact forest invertebrates directly through habitat alteration such as depletion of CWD, removal of organic layer and soil compaction (Ehnström 2001), loss of suitable habitat (Pettersson *et al.* 1995), isolation and fragmentation (Debinski and Holt 2000, Komonenet *et a*l. 2000), or indirectly by influencing the distribution and or abundance of competitors/predators (Örjan *et al.* 2007).

Within an organism's environment specific conditions are optimal for survival and reproduction. The role a species plays within this biotic and abiotic realm constitutes that species' niche (Whittaker *et al.* 1973, Rejmánek and Jenik 1975). The niche concept can encompass, in whole or in part, individual organisms, populations of organisms and species.

Two early theories in the concept of niche, which have since been refined (*e.g.*, Whittaker *et al.* 1973), include the fundamental niche, the total possible environmental space in which a species can exist in the absence of competition, and the realized niche, the niche that an organism occupies due in part to the influence of other species (McGill *et al.* 2006). Competition and other interactions, including predation, that occur between species define a species' realized niche (Alley 1982).

Biotic interactions that affect the distribution, abundance, and diversity of organisms can be considered to be beneficial, deleterious or neutral in terms of the effect of one species on another (Odum 1969). Competition has to be considered an important factor in determining the distribution, abundance and diversity of the populations that occupy a specific habitat (Diamond and Case 1986). It is important to note that niche overlap does not always result in competition (Alley 1982). As noted by den Boer (1979) in the case of carabids, taxonomically related species also tend to be ecologically related and thus tend to be found in the same types of habitat.

One method to measure interference competition in a community is to perform experiments that alter the composition of the community, *i.e.*, experiments that perturb the community (examples summarized in Connell 1983, Schoener 1983). A frequently used technique to achieve observable change in a measurable factor of a community is to remove one or more competitors. The theoretical response in this situation is ecological release: the increase of remaining competitors; a measurable indication of an increase in the use of resources that were negatively impacted by the removed competitor(s), and/ or; occupation of the habitat that was formerly occupied by the removed competitor(s) (Bender *et al.* 1984). Removing one species from a community to observe the response of another species is not

always possible; therefore, other methods are used to observe, infer, or otherwise detect interspecific competition (Keddy 1989). Altering a resource (frequently food/prey) that is hypothesised to be limiting in a competitive interaction is another method for experimentally determining if resource competition is occurring. In order to observe competition for a resource, that resource must be utilized by the competing organisms and limiting (Keddy 1989). Additional difficulties in interpreting the results of perturbation experiments may be important, as noted by Bender *et al.* (1984). For example, in studies using data on adult carabid numbers, observing the effect of competition may be difficult because competition and predation may be important at the larval stage of the life cycle but not readily observed in adults (*e.g.*, Currie *et al.* 1996).

In the absence of experimental evidence, observed trends in the distribution of species have been hypothesised to be the result of possible interference competition. Species that interfere with each other tend to be distributed in what has been described as a checkerboard distribution in contrast to a random distribution (Diamond 1975). Another technique that has been used to infer competition is character displacement, *i.e.*, the examination of physical characters of several species that occur in a delineated habitat. If competition among the species over evolutionary time was important in structuring the community and the resources that each species utilize, then there should be observable morphological differences between similar species related to their niche. This idea, however, has been examined and dismissed (Connell 1980).

Anthropological utilization of forested land occurs across several spatial scales from within stands to forests and landscapes, and extends temporally as dynamic forest processes, including anthropogenic disturbance, occurring over time (Burton *et al.* 2003).

Development of tools to monitor how forested ecosystems respond to disturbances is important for ecologically sustainable forest management. Biological indicators, or bioindicators, are potentially useful in this regard. Several requirements have been identified as desirable for biological indicators (Dale and Beyeler 2001). Invertebrates, particularly arthropods, have several attributes that make them suitable for such a role (Weaver 1995, Maleque *et al.* 2006). In particular, ground beetles (Coleoptera: Carabidae) have received much attention as useful indicators of impacts of anthropogenic disturbance in many forested ecosystems (Rainio and Niemelä 2003). Ground beetles or carabids are appealing research subjects for several reasons. They represent a well known taxonomic group that responds to environmental change, and is relatively easy and inexpensive to collect (Refseth 1980, Niemelä *et al.* 2000).

Carabid research has spanned all continents except Antarctica, where carabids do not currently occur (Ashworth 2001), and they have been studied in all habitat types (Lövei and Sunderland 1996). Furthermore, they occupy a wide spectrum of ecological niches and trophic levels (Lövei and Sunderland 1996), and have been demonstrated to have potential utility in indicating variations in biodiversity (Butterfield 1997) and in ecological and environmental conditions. Carabids generally are considered to occur in assemblages rather than in communities. Although interpretations differ (Morin 1999), communities are generally considered a group of populations that interact, while assemblages are populations that co-exist but do not necessarily interact. As carabids are a portion of the larger invertebrate community as a whole (Lövei and Sunderland 1996), the term assemblage will be used, except where cited authors use the term community or when referring to the larger invertebrate community.

Carabids have also been the subject of interest as an indicator group in forested ecosystems, grasslands and agroscapes (see Rainio and Niemelä 2003 for a review). For example, in a study examining the effect of forest succession on carabids, Baguette and Gerard (1993) found that the carabid assemblage composition in Belgian spruce plantations varied with stand structure and age. Brumwell *et al.* (1998) and Lemieux and Lindgren (2004) found that carabids in British Columbia also respond to successional changes in forests, and Koivula *et al.* (2002) found differences in species richness in regenerating stands of differing ages in Finland. Studies examining landscape level effects on carabid communities provide evidence of response to environmental conditions; for example, Halme and Niemelä (1993) examined the effect of fragmentation on carabids and found that large-bodied carabids were more abundant in contiguous forests in Finland than in forest fragments. Burke and Goulet (1998) had similar results when examining the response of carabids to forest fragmentation in Ontario; large-bodied species were more abundant, and species richness was higher in large fragments. Similarly, Abildsnes and Tømmerås (2000) found that different species of carabids respond differently to fragmentation of an old growth Norwegian forest.

Many carabid ecology studies ignore other surface-dwelling invertebrates (Lövei and Sunderland 1996). Within the epigaeic arthropod community, ants can play a particularly significant role (Lövei and Sunderland 1996; Laakso and Setala 1998, Laakso and Setala 2000, Punttila *et al.* 2004). They can reshape the landscape by mixing soil and distributing plant seeds. Additionally, ants affect community composition by exerting a strong predatory pressure on other invertebrates (Hölldobler and Wilson 1990). Established colonies can dominate their territories through aggressive behaviour which aids in their ability to acquire,

exploit and defend resources (Hölldobler and Wilson 1990). In many habitats ants may also numerically dominate the invertebrate community (Laakso and Setala 1998, 2000).

Ants are thermophilic (Hölldobler and Wilson 1990) and are therefore influenced by canopy cover (Punttila *et al.* 1991), which influences how much solar radiation reaches the forest floor (Huber and Baumgarten 2005). As forests grow, the amount of light penetration through the canopy is reduced. Reduction of solar radiation may influence dominance hierarchies among ant species (Cerda *et al.* 1998), and has been shown to lead to colony failure or abandonment when thermal requirements cease to be met (Higgins 2010). The change in the thermal environment of a stand likely influences the interactions between ants and other invertebrates, including carabids.

Ant colonies tend to occupy delineated territories, and many ant species defend these against both conspecifics from different colonies and heterospecifics (Hölldobler and Wilson 1990). Ants may alter the behaviour of other species, *e.g.*, spiders (Halaj *et al.* 1997) and even birds (Haemig 1996). Consequently, it is logical to expect that ants may significantly affect carabids.

While some studies make cursory mention of negative correlation between ants and carabids (Niemelä *et al.* 1992, Koivula *et al.* 1999, Koivula 2002, Koivula and Niemelä 2003), only a few studies have examined this interaction closely. Carabid adults appear to be non-significant as food items for red wood ants of the *Formica rufa* group (Skinner 1980), but Reznikova and Dorosheva (2004) demonstrated that the presence of ants can alter the behaviour of carabids. They showed that ants act aggressively towards carabids, and that different species of carabids may respond differently to the presence of ants by altering movement patterns and/or protecting limbs. Hawes *et al.* (2002) showed that the presence of

ants affects species composition and distribution of carabids, although the mechanisms causing these changes are not clear. The overall objective of my research was to examine the potential effect of ants on carabid assemblages at different successional stages of forest development after harvesting.

Several collection techniques have been employed in epigaeic invertebrate research, depending on the goal of the research. The predominant technique utilized in ecological studies of carabids is passive capture in pitfall traps of various designs, a technique that also can be used to collect ants. Passive capture relies on invertebrates falling into a neutrally attractive trap, which gives a measure of abundance that is generally inseparable from activity. This is due to the two requirements of pitfall trapping: 1) carabids are present (abundance), and; 2) they are able to move into the pitfall trap (activity), resulting in the commonly used measure "activity-abundance" (Spence and Niemelä 1994). The "standard" or "conventional" pitfall trap is any container with a round opening placed with the opening flush with the ground (Greenslade 1964). Numerous variations of pitfall trap designs have been tested and compared for their effectiveness in collecting carabids (Greenslade 1964, Epstein and Kulman 1984, Spence and Niemelä 1994, Lemieux and Lindgren 1999, Abensperg-Traun and Steven 1995, Work *et al.* 2002, Koivula *et al.* 2003, and Pearce *et al.* 2005). Variation among trap types was observed in the quantity of carabids collected, with larger traps tending to catch more beetles (Work *et al.* 2002, Koivula *et al.* 2003) and ants (Abensperg-Traun and Steven 1995), although this relationship is not linear (Work *et al.* 2002). Nordlander traps provided a better reflection of species richness (Pearce *et al.* 2005), while mitigating other pitfall trap associated difficulties.

Pitfall traps do not provide data pertaining to the absolute density of carabids (Andersen 1995, Lang 2000), but on activity abundance (Spence and Niemelä 1994). Perner and Schueler (2004), however, propose that using a nested cross array trapping pattern, and fitting catch data to a single hyperbolic function may provide density estimates. Maehara (2004) found that pitfall catches of *Carabus insulicola insulicola* Chaudoir in an enclosed population correlated with the population density.

Carabids tend to move at random across the landscape (Baars 1979; Drach and Cancela da Fonseca 1990, Lövei and Sunderland 1996; Firle *et al.* 1998), and pitfall trapping is therefore an appropriate technique for sampling. Movement is influenced by habitat, ambient temperature (Baars 1979) and hunger, since carabids utilize random search to locate prey items (Wallin and Ekbom 1994; Lövei and Sunderland 1996). The movement tends to result in a linear increase in the area covered by beetles over time, but not necessarily in point to point distance traveled (Firle *et al.* 1998). Carabids respond to encounters with inhospitable or unfavourable environments by fleeing, and they then frequently move in a more linear direction than observed in more favourable environments (Baars 1979). In favourable environments it is unlikely that carabids moving exclusively by ambulatory means travel distances greater than 100m in a season (den Boer 1990). Movement patterns may be highly variable between species that fill different habitat niches, *e.g.*, forest generalists vs. forest specialists (Brouwers and Newton 2009). The area covered by individuals may be at a scale of hectares as suggested by movement modeling (Firle *et al.* 1998), but experimental and observational data are currently lacking (Brouwers and Newton 2009).

Pitfall trapping is a cost effective and repeatable method of capture which has proven particularly suitable for the collection of carabids (Spence and Niemelä 1994) and ants (Melbourne 1999) provided that biases and limitations are understood (Koivula *et al.* 2003). Thus, pitfall trapping has been extensively utilized for the purpose of collecting and examining carabid activity abundances, carabid assemblage composition (Lövei and Sunderland 1996) and the activity abundance and species composition of ants (Melbourne 1999).

The purpose of this study is to: (1) examine changes in carabid assemblages in post-harvest systems at different successional stages in west central British Columbia sub boreal spruce stands (Chapter 2); (2) examine the effect of ants on carabid abundance (Chapter 3); and (3) to experimentally examine the relationship between carabids and the ant *Formica aserva* Forel in a young regenerating stand (Chapter 4).

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Chapter Two

Effect of forest succession on carabid (Coleoptera: Carabidae) assemblage structure in post-harvest stands in sub boreal spruce forests of west-central British Columbia

I examined carabid beetle (Coleoptera: Carabidae) assemblages in post-harvest and unharvested sub boreal spruce (SBS) stands in west central British Columbia, Canada. To obtain a description of carabid assemblages in successional SBS forest, carabid species composition, the seasonal activity of abundant carabid species and the differences in activity-abundance of males and females, I installed 750 Nordlander pitfall traps in 10 stands encompassing a gradient in canopy cover from 0% to 100%. A total of 4801 individual carabids, representing 31 species, were collected over 12 weeks. Carabid assemblages in SBS stands are influenced by vegetation and structure. Non-metric multidimensional scaling revealed four carabid assemblages, each associated with different vegetative characteristics. Variables associated with stand succession (canopy cover, vegetation diversity, and correlations along a gradient of grass-dominated ground cover) accounted for most of the variation in the ordination. Seasonal activity and sex ratios of eight common species showed significant within-species variation in standardized mean activity-abundance for seven species. In the SBS, seasonal activity of individual species, as well as forest type associations related to canopy cover, differed from findings of other studies with similar species assemblages. Canopy cover, which influences temperature and relative humidity, shows strong influence over the species composition of carabid assemblages in regenerating stands although other factors not examined here may also influence the distribution of species within assemblages.

Introduction

Lindroth's (1961-69) comprehensive taxonomic monograph on the carabid beetles of Canada and Alaska provides an excellent taxonomic base for carabid studies in British Columbia (B.C.), however, knowledge of the carabid assemblages in west-central B.C. is poor. A study undertaken near Smithers, B.C. in harvested, high-elevation stands in the Engelmann Spruce-Subalpine Fir biogeoclimatic zone (Meidinger and Pojar 1991), to examine the immediate (2 to 4 years post-harvest) response of carabids to partial harvesting (Lemieux and Lindgren 2004), is the only example of carabid research in this region.

Species inventories are to understand the distribution of species, relationships among species, effects of landscape structure and effects of anthropogenic disturbances, such as forestry (Niemelä *et al.* 1994), on biodiversity (Jenkins 1988). Baseline inventories of carabids have yet to be completed for different successional stages of forest regeneration in west-central B.C. Without this knowledge it is impossible to assess the possible long-term effects that harvesting may have upon carabids. Comparing the assemblage in regenerating stands shortly after harvest to unharvested stands provides information pertaining to the immediate effect of forest harvesting on carabids. Examining carabid communities in regenerating forests at different intervals after harvesting provides insights into ecological processes involved in managed forests (Niemelä *et al.* 1993, Atlegrim *et al.* 1997, Ings and Hartley 1999, Koivula *et al.* 2002, Heyborne *et al.* 2003, Vance and Nol 2003, Brouat *et al.* 2004, de Warnaffe and Lebrun 2004). Hence, knowledge of the fauna that inhabits regenerating and mature forested stands is paramount to the understanding of ecological processes that shape the boreal forests (Korpilahti 1996).

Carabids are distributed non-randomly across the landscape (Niemelä and Halme 1992, Niemelä *et al.* 1992). Therefore, microhabitat associations provide information as to where carabids tend to be found. Variation in carabid communities has been linked to light penetration (Niemelä *et al.* 1988, Abildsnes and Tømmerås 2000) or solar radiation (Huber and Baumgarten 2005). Penetration of light in forested stands is directly related to canopy closure (Huber and Baumgarten 2005), which in turn has been identified as a variable which influences carabid activity-abundance and assemblage composition (Magura and Tothmeresz 1997, Brumwell *et al.* 1998, Humphrey *et al.* 1999, Jukes *et al.* 2001, Koivula 2002, Koivula *et al.* 2002, Magura 2002, Magura *et al.* 2002, Heyborne *et al.* 2003, Lassau *et al.* 2005).

Several studies have found shifts in carabid assemblage structure post-harvest (Niemelä *et al.* 1993, Atlegrim *et al.* 1997, Beaudry *et al.* 1997, Butterfield 1997, Koivula 2002, Koivula *et al.* 2002, Heyborne *et al.*. 2003). Niemelä *et al.* (1992) proposed a conceptual model of carabid species succession. The model predicts a loss of mature-forest species, a decrease in forest-generalist species and an increase in open-ground species in early succession post-harvest. Open-ground species then decline as the forest matures, while forest-generalists increase. Eventually the open-ground species will drop out of the community and forest-generalists will be dominant. As the forest regains a mature structure, mature-forest specialists will reappear, although this has not been readily observed (Niemelä *et al.* 1993, Spence *et al.* 1996, Heyborn *et al.* 2003) and may not occur if source populations are no longer available to provide individuals to colonize what may appear to be suitable habitat (Niemelä *et al.* 1993, Spence *et al.* 1996). Most research has occurred relatively early in the forest succession after disturbance, however. In general the model suggested by Niemelä *et al.* (1992) has been supported by several studies (Niemelä *et al.* 1992, Niemelä *et*

al. 1993, Atlegrim *et al.* 1997, Koivula *et al.* 2002, Koivula and Niemelä 2003). Relating carabid faunal groupings specifically to forest canopy closure gradients has been suggested as a more appropriate method, however, since it reflects the habitat requirements of forest species, and coincides with patterns observed in other studies (Koivula 2002).

The pattern of carabid response to deforestation and subsequent regeneration is not universal. Heyborn *et al.* (2003) noted that carabids associated with mature forest conditions were not re-establishing when the vegetation succession was moving towards becoming a closed forest. Also, carabids considered mature-forest species were not lost in young post-harvest stands at high elevations (Pearsall *et al.* 2003, Lemieux and Lindgren 2004), indicating that factors other than vegetation structure may be important.

The objectives of this study were to: characterize the carabid assemblage in a cool forest ecosystem classified in the sub-boreal spruce biogeoclimatic zone (SBS) (Meidinger and Pojar 1991), examine the effect of clearcut harvesting on carabids, and document how carabid communities change in post-harvest stands as forest succession proceeds and stand canopies close.

Methods

Site Selection

Ten stands (study sites) were selected in the SBS biogeoclimatic zone in west central B.C. near the village of Houston. This biogeoclimatic zone generally occurs between 800 m to 1300 m above sea level in central B.C. between latitudes 51° 30' and 59° N. Mean annual temperatures range between 1.5°C and 5°C, with 2-5 months having average temperatures below 0°C. *Picea glauca* (Moench) Voss x *Picea engelmanni* Parry ex Engelm. and *Abies lasiocarpa* (Hook.) Nutt. are the dominant climax tree species, with *Pinus contorta* Dougl. ex

Loud. var. *latifolia* Engelm a common seral species (Meidinger and Pojar 1991). Natural grasslands are rare and only occur scattered in dry valley bottoms. Within the SBS, ten sub-zones have been described. This study was conducted in the moist-cold variant (mc), which is typified by a shrub/herb layer dominated by *Cornus canadensis* L., *Vaccinium membranaceum* Dougl. ex Torr., *Lonicera involucrata* (Richards.), *Viburnum edule* (Michx.) Raf., *Rubus pedatus* Sm., *Petasites frigidus* var. *palmatus* (Ait.) Cronq., and the mosses *Ptillium crista-castrensis* (Hedw.) De Not., *Pleurozium schreberi* (Brid.) Mitt. and *Hylocomium splendens* (Hedw.) Schimp. (Meidinger and Pojar 1991).

Study sites were required to be within the operating area of West Fraser's Houston Forest Products Division (HFP West Fraser) for logistic reasons associated with funding in 2005. Possible sites were identified using HFP West Fraser's database, and were restricted to lodgepole pine-leading stands within the SBS. Additionally, sites were selected in the following post-harvest age classes: 2 years post-harvest (yph), 12 yph, 16 yph, >25 yph and non-harvested. Approximate age classes were selected as they represent shifts in vegetation structure from open ground to shrub, shrub to low canopy, low canopy and closed canopy, encompassing a gradient ranging from no canopy (0% coverage) to closed canopy (100% coverage). Post-harvest sites with a developing high canopy did not exist or were inaccessible in the SBS within the operating area of HFP West Fraser. Within each site, a one hectare plot was randomly positioned at least 50m away from an edge (*i.e.*, road, stream, abrupt elevation change, forest or cut block). The exact study site locations are listed in Appendix I.

Pitfall Sampling

Plots were placed within cut blocks to avoid inclusion of anthropogenic features such as spur roads, skid trails and landings, and natural features such as streams, swamps or substantial bodies of standing water, that would exclude trapping. An intense sampling protocol was used to attempt to provide fine scale data regarding variation in activity-abundance and habitat use. Three 80m long transects were established, each starting at a randomly selected point within each 1ha plot. Each transect ran at a randomly determined bearing not constrained by the plot boundary. Five trapping clusters were established along each transect, each consisting of a central pitfall trap at 20m intervals, two satellite traps 3m from the central trap along the transect, and an additional two traps 3m from the transect at 90° and 270° from the transect (Figure 1).

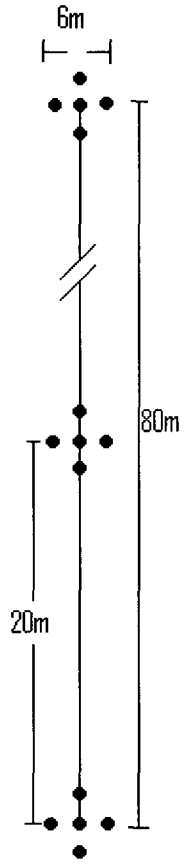

Figure 1: Diagram of pitfall trapping transect. Closed dots indicate pitfall traps.

Thus, trapping clusters were separated by a minimum of 14m, as a distance between 10m and 20m is required to mitigate trapping effects between traps (Digweed *et al.* 1995) while providing fine-scale resolution.

Pitfall traps were a Nordlander type (Nordlander 1987) modified after Lemieux and Lindgren (1999). Each trap was constructed out of an 8oz translucent multipurpose container (VWR catalogue number 4333-002) with a diameter of 8cm and depth of 7.5cm. Fourteen 12mm long × 6mm high entrance holes were punched below the lid of the container using a hole punch. Traps contained a 90mL of 25% propylene glycol solution. Samples were collected and the fluid replaced every 14 days from May 25, 2005 until August 28, 2005.

Specimens were transferred to specimen cups for transport to the lab, where they were rinsed in a soap and water solution to remove debris, then rinsed in distilled water to remove soap residue. Carabids and ants from each individual pitfall trap were identified and then placed in labelled vials containing 70% ethanol. Several specimens from each species (a minimum of 10 where possible) were pinned and labelled. Voucher specimens have been deposited at the Strickland Entomological Museum, University of Alberta, Edmonton, Alberta, and the Royal BC Museum, Victoria, British Columbia.

Vegetation Sampling

The composition of vegetation was recorded at each pitfall trap in an approximate $1m^2$ area using digital photographs taken from a height of approximately 1m directly above the trap. From these images the dominant ground cover and the vegetation density was assessed. Vegetation density was categorized as sparse, low, moderate, or high. Additionally, the presence of coarse woody debris (CWD) (pieces of dead wood with diameters greater than or equal to 10cm), stumps, large rocks, litter, fine woody debris (downed wood less than 10cm and greater than or equal to 0.5cm in diameter), wood in advanced decay and exposed mineral soil were recorded as they appeared in the photos.

Data pertaining to canopy cover and vegetation vertical cover were collected for fifteen sampling points located in each of the ten study stands. Vegetation species were recorded as present or absent at each trap. The vegetation presence/absence data were then summed for all five traps at each sampling point. Thus a score of zero to five was possible for each species at each sampling point; five being locally ubiquitous and zero being locally absent.

Canopy cover (the percent of the ground area shaded by overhead foliage) was assessed using a convex spherical densiometer (Forest Densiometers, Model – A, Arlington, Virginia), which have been shown to be reliable for assessing canopy cover (Lemmon 1957). From the center of each sampling point, four readings were taken from waist height (approximately 1m), facing north, east, south and west (Lemmon 1957). Mean values were calculated for each sampling point. Due to the ease and speed of use, low cost and transportability, vertical vegetation cover was assessed using a forest cover pole 2m in height divided into ten 20cm sections. The cover pole was positioned at the sampling point center. Cover was assessed from a distance of 4m and a height of 1m from north, east, south and west aspects. Sections more than or equal to 25% obscured by vegetation were considered covered and counted as such (Griffith and Youltie 1988).

Data Analyses

Carabids were identified according to Lindroth (1961-1969). Each individual carabid was also sexed. Confirmation of species identification was undertaken at the Canadian Forest Service, Northern Forestry Centre, and the Strickland Entomological Museum, University of Alberta, both in Edmonton, Alberta.

Statistical analyses were done using the SYSTAT (v. 11) (SYSTAT Software, Inc., Richmond, CA) software package, the only exception being non-metric multidimensional scaling which were done using the PC-ORD (PC-ORD v.5, MjM Software, Gleneden Beach, OR) software package.

Seasonal variation was examined for the most abundant species, defined as those that comprised at least 2% of the total carabid catch. For these species the actual catch per 14 day trapping period, and five-trap trapping cluster, was standardized to a single day and then

multiplied by 14 to give the standardized catch for a single trapping cluster for a two week trapping period. Repeated measures ANOVAs were performed to examine differences in the seasonal activity-abundance of male and females. Post-hoc tests to determine seasonal differences in the mean activity-abundance between males and females over the trapping period were performed when the null hypothesis was rejected using univariate F tests. Alpha levels were corrected using a Bonferroni adjustment in order to account for multiple comparisons (Tabachinick and Fidell 2001).

Carabid data were standardized to 100 trap-days prior to analysis. Standardization was the sum of the five traps in each trapping cluster divided by total number of days the trap cluster was operational multiplied by 100. Missing, destroyed, or damaged traps for each cluster were accounted for by multiplying the summed total of the trap cluster by 1, plus 0.2 for each missing, damaged or destroyed trap. This reduced the comparative influence of lower trap days for traps that were destroyed, damaged or otherwise disturbed during a 14 day sample period. Relationships among vegetative structure parameters were assessed by examining correlations among the vegetation cover and canopy cover. Relationships were then used to group the vertical vegetation data into three groups: Low – cover measured on the lower 20cm – 60cm of the cover pole representing herbaceous vegetation and forbs, Shrub – cover measured between 60cm – 100 cm on the cover pole representing shrubs, and High – cover measured above 100cm on the cover pole, representing mature shrubs and low branches/crowns.

Three measures of diversity were calculated for carabids in three canopy cover groups: no canopy (0 to 10% coverage), developing canopy (11 to 89% canopy coverage) and closed canopy (90 to 100% canopy coverage). Measures of gamma diversity (γ)

(landscape level diversity; the sum of all species collected), and alpha diversity (α) (species richness per trap cluster; sum of the species collected at a single trap cluster), were calculated. Beta diversity (β) (heterogeneity in the data=α divided by γ), was also calculated (McCune and Grace 2002). ANOVA was used to examine differences in alpha diversity of the three canopy cover groups.

Assemblage data were visualized using NMS (McCune and Mefford 1999) with the goal of examining clusters of species, or species-groups and to explore variation in the assemblages. All NMS ordinations were run using distance matrices constructed using Sørensen distance measures. Each NMS ordination involved 50 runs, each with random and real data to ensure reliable ordination. Ordinations were considered reliable if they were significantly different than random, as determined by Monte Carlo analysis, but similar to the other ordinations run on the same data set. Determination of the number of dimensions appropriate for the data was achieved by examining NMS scree plots and selecting the number of axes beyond which reductions in stress is small (McCune and Grace 2002). Once the number of axes for interpretation had been determined, a final ordination was run as recommended by McCune and Grace (2002).

Non-metric multidimensional scaling was run to produce an ordination of sample points in carabid species space. Ordinations were compared to elucidate differences based on species selections, *i.e.*, does species selection influence the picture provided though NMS. Second matrix (explanatory variables) correlations were examined, with structural variables, to attempt to provide possible explanations for observed axes correlations.

Results

The total carabid catch, collected from May 25, 2005 until August 28, 2005, consisted of 31 species of carabids and 4801 individual specimens (Table 1). Nine species, *Scaphinotus marginatus* (Fischer von Waldheim), *S. angusticollis* (Fischer von Waldheim), *Calathus ingratus* Dejean, *C. advena* (LeConte), *Synuchus impunctatus* (Say), *Elaphrus lapponicus* Gyllenhal, *Pterostichus adstrictus* Eschscholtz, *P. riparius* Dejean and *Trechus chalybeus* Dejean, comprised 77.0% of the total catch. The remaining 22 species each contributed less than one percent of total catch.

Season and Gender

The only species where the variation in mean activity-abundance between sexes over the trapping season was not significant was *T. chalybeus* (Figure 2h, Appendix II). *Scaphinotus* species (Figure 2a,b; Appendix II) have higher activity-abundance in late summer, while three species (Figure 2d, e, f; Appendix II) have higher activity-abundances in spring. *Synuchus impunctatus* (Figure 2g; Appendix II) had a peak in activity-abundance in the early summer and *P. adstrictus* (Figure 2c; Appendix II) activity-abundance increased from spring to late summer with a large number of males collected in the first trapping period.

Table 1: Summary of carabid species collected in successional sub-boreal spruce forests in west central BC, during the spring and summer of 2005. Catch for each species is standardized to number of individuals per 100 trapping days

Species	Species codes	Females	Males
Trachypachus holmbergi Mannerheim	TRAHOL	2.38	2.38
Scaphinotus angusticollis (Fischer von Waldheim)	SCAANG	370.36	411.31
Scaphinotus marginatus (Fischer von Waldheim)	SCAMAR	412.02	655.48
Carabus taedatus Fabricius	CARTEA	3.57	1.19
Notiophilus sylvaticus Eschscholtz	NOTSYL	17.14	18.69
Elaphrus clairvillei Kirby	ELACLA	7.14	1.43
Elaphrus lapponicus Gyllenhal	ELALAP	87.98	80.71
Patrobus fossifrons (Eschscholtz)	PATFOS	15.48	20.00
Trechus chalybeus Dejean	TRECHA	476.79	301.55
Bembidion grapii Gyllenhal	BEMGRA	4.64	5.71
Bembidion fortestriatum (Motschulsky)	BEMFOR	5.71	2.86
Amerizus oblongulus (Mannerheim)	AMEOBL	4.05	0
Pterostichus herculaneus Mannerheim	PTEHER	1.43	1.43
Pterostichus adstrictus Eschscholtz	PTEADS	373.57	198.93
Pterostichus riparius Dejean	PTERIP	202.98	114.40
Pterostichus brevicornis (Kirby)	PTEBRE	8.81	0
Pterostichus castaneus (Dejean)	PTECAS	7.62	3.81
Stereocerus haematopus (Dejean)	PTEHAE	5	2.62
Calathus ingratus Dejean	CALING	87.62	31.19
Calathus advena (LeConte)	CALADV	653.33	322.26
Synuchus impunctatus (Say)	SYNIMP	514.29	558.21
Agonum gratiosum (Mannerheim)	AGOGRA	2.62	0
Agonum affine Kirby	AGOAFF	8.57	14.29
Agonum cupreum Dejean	AGOCUP	0	2.86
Amara sinuosa (Casey)	AMASIN	19.76	17.14
Amara erratica (Duftschmid)	AMAERR	41.26	24.88
Harpalus animosus Casey	HARANI	4.05	0
Harpalus somnulentus Dejean	HARSOM	9.05	10.48
Bradycellus conformis Fall	BRACON	5.71	8.57
Trichocellus cognatus (Gyllenhal)	TRICOG	0	1.43
Lebia moesta LeConte	LEMMOE	7.38	2.62
Total Standardized Catch			6112.74

Examination of the seasonal trends in activity-abundance for male and female carabids indicated male activity-abundance differed significantly from females (or *vice versa*) during at least one trapping period for all species except *T. chalybeus* (Figure 2; Appendix II). Additionally seasonal effect on activity-abundance was significant in five of the eight abundant species (Figure 2; Appendix II). Post-hoc (F test) examination indicated that seasonality significantly affected both males and females for *S. marginatus*, *C. advena*

and *S. impunctatus*. Male *S. angusticollis* were significantly influenced by seasonality, as were female *P. adstrictus, P. riparius* and *C. ingratus* (Figure 2; Appendix II).

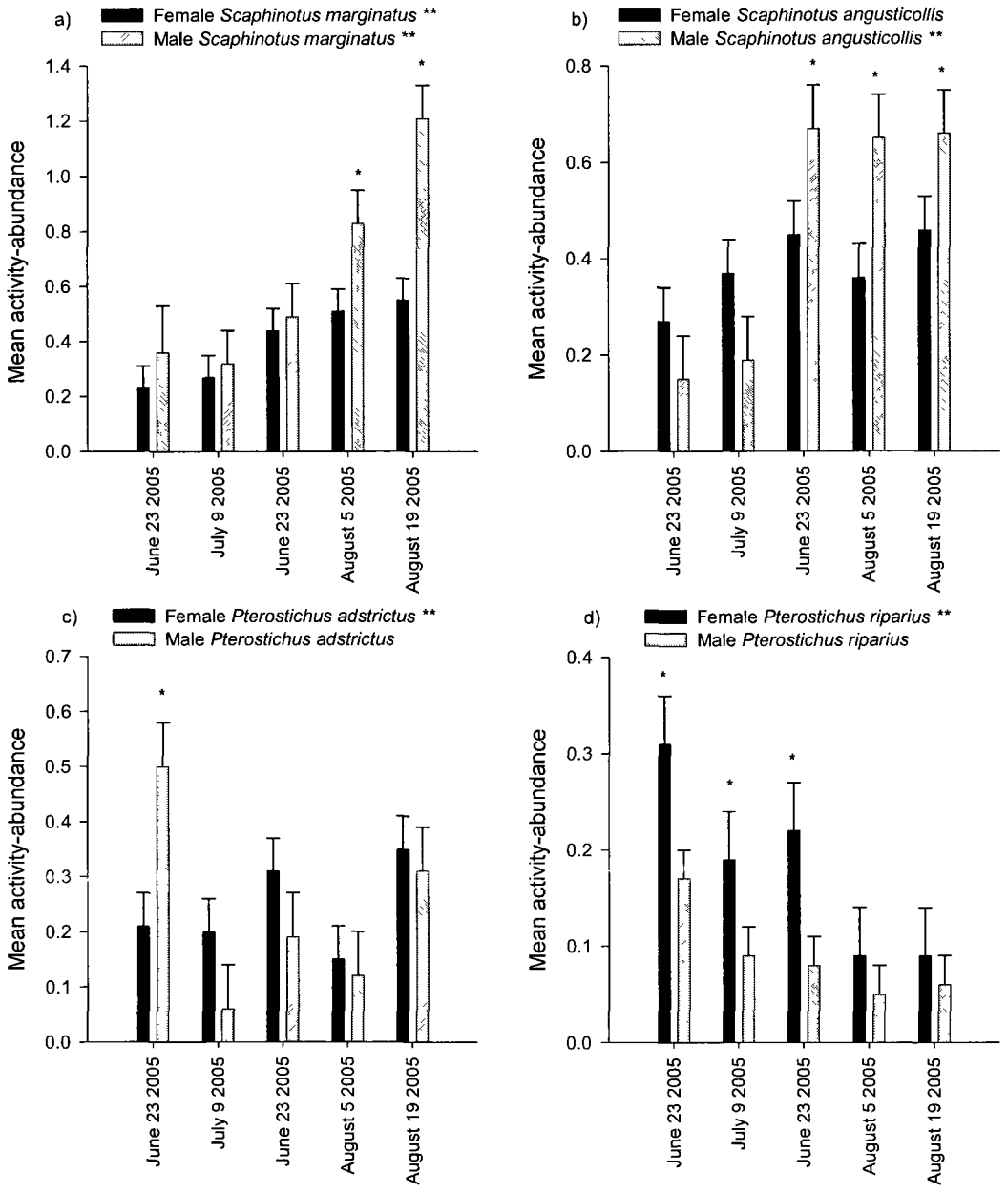

Figure 2 a - d: Seasonal variation in mean activity-abundance (± SEM) for males and females of the most abundant (>2% of total catch) species of carabid standardized to 14 trap days.
***= significant difference between sexes for a trapping period (α=0.025)**
****** **= significant effect of season (α=0.05).**

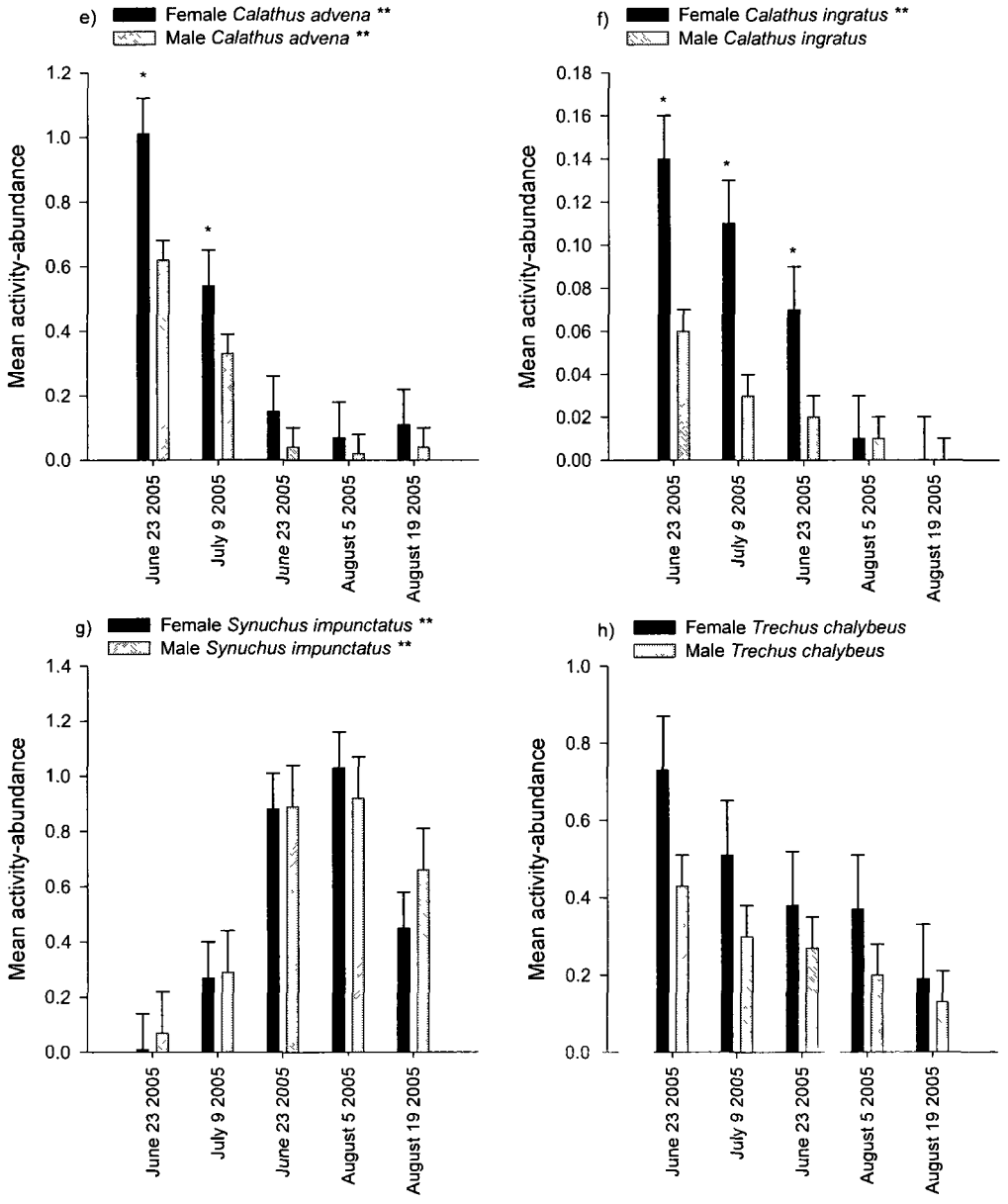

Figure 2 continued e - h: Seasonal variation in mean activity-abundance (± SEM) for males and females of the most abundant (>2% of total catch) species of carabid standardized to 14 trap days.
*** = significant difference between sexes for a trapping period (α=0.025)**
**** = significant effect of season (α=0.05).**

Vegetation Cover

There was no correlation between mean canopy cover and vertical vegetation cover classes of 0 - 20cm, 21 - 40cm, and 41 -60cm (r = -0.053, -0.114, -0.010, respectively), and only weak positive correlations between mean canopy cover and vertical vegetation cover classes of 61 - 80cm and 81 - 100cm (r = 0.210 and 0.254, respectively). For mean canopy cover, and the five remaining vertical vegetation cover classes >101cm in height, there was a stronger correlation (r = 0.335, 0.399, 0.364, 0.327, 0.407, respectively). All correlations among the vertical vegetation cover classes were positive, with adjacent classes tending to be strongly correlated, *i.e.*, $r > 0.7$. Based on these results, vegetation height classes were pooled into four classes, 0 - 20cm, 21 – 60cm, 61 – 100cm, and >101cm. Values for vertical vegetative cover were then ranked.

A sigmoidal regression to model canopy cover and stand age used the function:

$f = a/(1+\exp(-(x- x_0)/b))$

The model yielded the best fit when a = 96.65; b = 0.37; x_0 = 3.04 (adjusted R^2 = 0. 91; $F_{(2, 149)} = 784.86$; $P < 0.0001$) (Figure 3). The plot showed that 16yph stands displayed great variation in canopy cover.

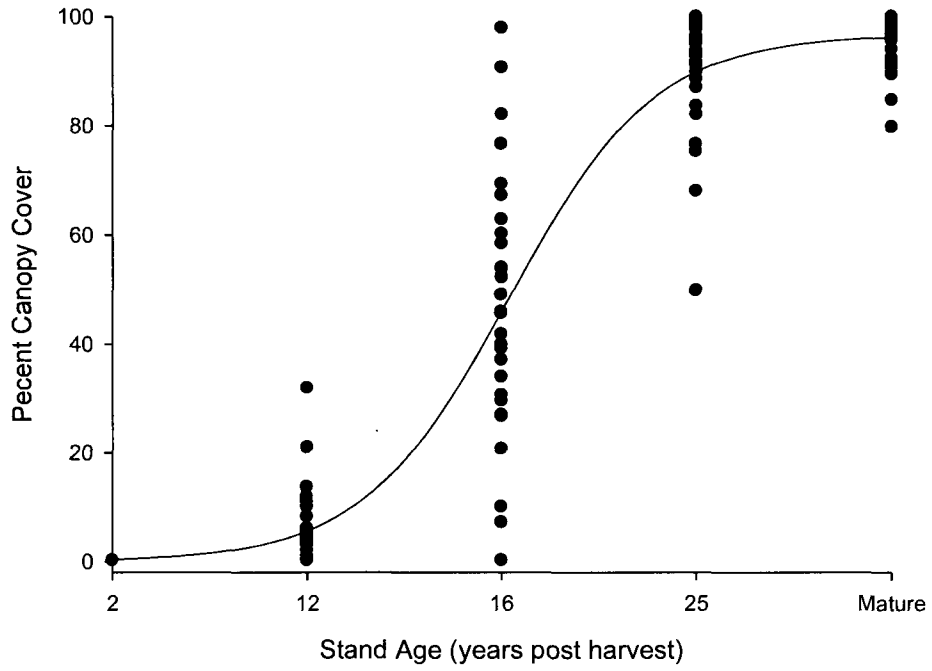

Figure 3: Sigmoidal relationship between percent canopy cover and stand age (years post-harvest): adjusted R^2 = 0. 91; $F_{(2, 149)}$ = 784.86; P < 0.0001.

Diversity

Significant differences in mean carabid alpha diversity between canopy cover classes were noted (R^2 = 0.07; $F_{(2,148)}$ = 5.8; P = 0.004). Post-hoc examination (Tukey's) indicated that plots with less than 10% canopy cover had significantly greater mean diversity (P = 0.002) than plots with developing canopies (11-89% canopy cover). Plots with closed canopies (>90% canopy cover) had mean alpha diversity values slightly greater than plots with developing canopies, but the differences were not significant. Beta diversity followed the same trend (Table 2).

Table 2: Diversity measures calculated for carabid assemblages sampled in 2005. Mean carabid diversity is calculated by plot canopy cover classes (no canopy, developing canopy, closed canopy) Diversity measures are defined in the text.

Diversity Measure	All plots	Open canopy	Developing canopy	Closed canopy
α	4.8	5.39	4.11	4.86
β	0.15	0.17	0.13	0.16
γ	31	31	31	31

Assemblage Ordination

Data pertaining to species collected in fewer than 5 plots were discarded prior to NMS ordination of the carabids. Removal of species with relatively few collections was done to increase the stability of the ordination (McCune and Grace 2002). This resulted in removal of 10 carabid species (*Trachypachus holmbergi, Carabus taedatus, Pterostichus herculaneus, Trichocellus cognatus, Harpalus animosus, Agonum gratiosum, Amerizus oblongulus, Agonum cupreum, Elaphrus clairvillei, Patrobus fossifrons*) leaving 21 carabid species in the ordination. Examination of the NMS scree plot indicated that two-axis solutions could be obtained for the ordination with a final stress of 20.34. Species points indicate the relative orientation of a given species in relation to carabid assemblages, it is important to note that the position should not be considered an absolute point, but rather a central point within a cloud of points representing the species distribution relative to all other species in the ordination (Figure 4). The percent of the total variance in the NMS ordination explained by structural variables on the x axis was 18.8%, while the y axis explained 37.0% (Figure 4). NMS correlations (Figures 4) can be found in Appendix III. The x axis includes variation contributed by positive correlations with a high grass component of ground cover.

The y axis includes variation contributed by positive correlations with canopy cover, high needle component of ground cover, diversity in vegetation and a negative correlation with slash; residual fine woody debris left on the ground after harvest, consisting primarily of fine twigs, small branches and cones.

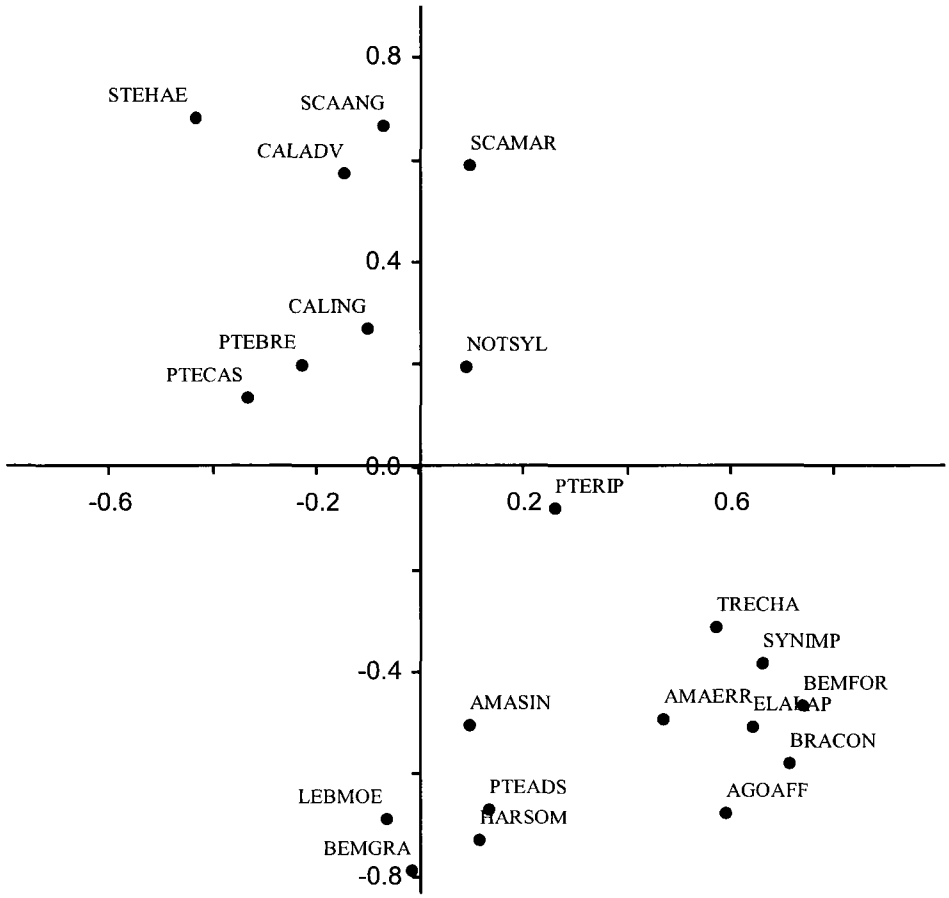

Figure 4: NMS ordination of carabid assemblages. Axes scales are the raw correlation coefficients. Species codes consist of the first 3 letters of genus and the first 3 letters of species names (see Table 1).

Examination of the association between canopy cover and carabid activity-abundance yielded little information that was not captured in the ordination (Figure 4). In the case of *P. riparius*, however, the highest activity-abundance was in the highest canopy

cover plots, with lower activity-abundance in the lowest canopy cover classes. Zero individuals of this species were collected in plots with 43% – 79% cover (Figure 5).

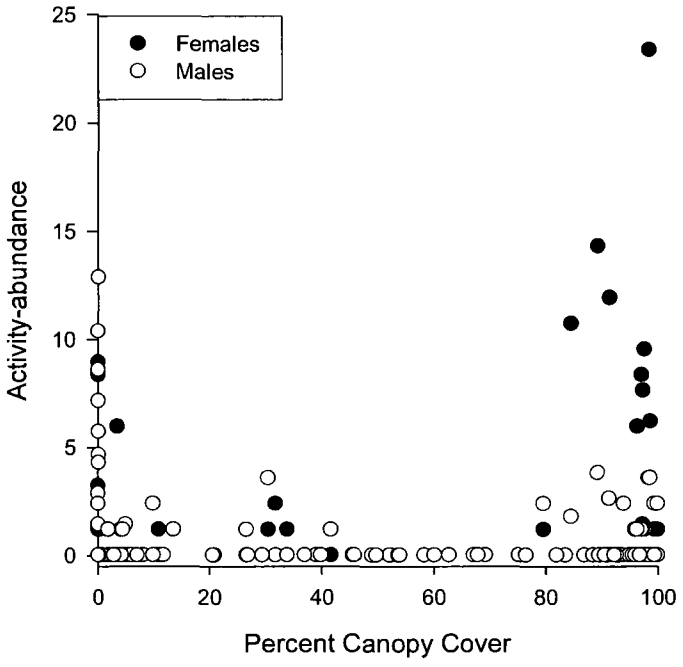

Figure 5: Relationship between activity-abundance of *Pterostichus riparius* and canopy cover.

Discussion

Seasonal variation

Seasonal activity-abundances of common species differed from those reported in some studies, but not others. For example, *Synuchus impunctatus* had a peak in activity-abundance in late summer, which is consistent with findings in forests of northeastern Wisconsin and the Upper Peninsula of Michigan (Werner and Raffa 2003). Niemelä *et al.* (1992b) observed high catches in early spring and late summer for *Scaphinotus marginatus*. This differs from the late summer peak in activity-abundance observed in my study and that of Pearsall *et al.* (2003) on Vancouver Island. The differences are most likely influenced by

environmental variation related to regional differences in mean temperature and length of snow-free period and degree days (Werner and Raffa 2003), none of which were actively sampled in my study. Niche segregation, however, may also play a role, in that seasonal segregation of activity may alleviate the potential for competition in species that would otherwise occupy overlapping niches (Loreau 1987). Activity-abundance of *Calathus ingratus* in my study area was highest in early summer, unlike Werner and Raffa's (2003) findings, where this species had the highest activity-abundance in late summer. Seasonal variation of activity-abundance of the largest carabid, *Scaphinotus angusticollis,* was similar to the trends observed by Pearsall *et al.* (2003) on Vancouver Island.

Variation in carabid activity-abundance during snow-free months has been attributed to increased activity during the breeding season, variation in prey item abundance (Loreau 1987, 1988), preferred thermal environment (Crist and Ahern 1999), and habitat. Alteration of the landscape may cause a shift in seasonal activity-abundance in some species of carabids (Holliday 1991, Crist and Ahern 1999), *e.g.*, wide-ranging generalist species may have plastic seasonal abundance that varies with habitat. In species that display consistent trends in seasonal abundance across their geographic range, regardless of the habitat they occur in, seasonal variation is likely influenced by factors other than habitat. Studies reporting seasonal variation exist for forest carabids east of the continental divide (Niemelä and Spence 1991, Niemelä *et al.* 1992b, Niemelä *et al.*1993, Werner and Raffa 2003), and for species collected west of the continental divide (Lindroth 1961-1969, Pearsall *et al.* 2003). This variation in species activity-abundance over snow free months is of concern as proportional catch data may be skewed with shifting species activity-abundance patterns especially in studies that utilize small sampling windows.

Gender Differences

Significant differences between gender activity-abundance, in at least one trapping period, were noted for all abundant carabids except *T. chalybeus*. The difference in activity-abundance was observed for both males and females, except in the case of female *S. angusticollis*. Assumption of a 1:1 sex ratio is frequently used, and deviation from that ratio may indicate differences in activity (Rolando *et al.* 2008) and/or habitat use (Kagawa and Maeto 2009) between the sexes. It is also possible that deviation from a 1:1 sex ratio may provide insight into prey abundance, as locomotion in carabids has been linked to feeding state (Wallin and Ekbom 1994, Firle *et al.* 1998, Szyszko *et al.* 2004) and in increases in female carabids nutritional requirements during egg production (Van Dijk 1994). Szyszko *et al.* (2004) makes a compelling argument for sex ratio being relating to habitat quality in the case of *Carabus hortensis* L, but locomotion (Reznikova and Dorosheva 2004), habitat selection, and sex ratios in other species may also be influenced by other organisms, *e.g.*, ants (Hawes *et al.* 2002).

Significantly higher female activity-abundance in the spring likely is related to over-wintering female adults emerging and immediately looking to increase their fat stores for egg production and spring breeding. Higher activity-abundance of males late in the summer may relate to dispersal. While not presented here, there were no notable trends relating habitat and differences in female to male ratios. In other words, if female activity-abundance was significantly greater than male activity-abundance (or vice versa) similar proportional differences were observed across all sampled stands. The only exception was *P. riparius* (Figure 5), for which activity-abundance of females was notably higher under closed canopy conditions.

Influence of canopy cover / stand age and vegetation

Canopy cover (the percent of the ground area shaded by overhead foliage), has been suggested as a useful measure of habitat differences in wildlife habitat studies, including studies of carabid habitat associations (Koivula 2002).. The relationship between canopy cover and stand age in conifer-dominated forests generally adheres to a sigmoidal relationship (Hamilton 1988), as observed in this study (Figure 3).

Vegetation composition can provide information pertaining to site characteristics such as moisture, soil types, nutrients and light (Wang 2000). Additionally, vegetation cover may influence the trapability of carabids (Baars 1979), and vegetation density may influence carabid activity-abundance (Brose 2002). A single strong successional gradient was noted in NMS. Dispersion observed among NMS pitfall cluster correlations in middle age class stands is likely due to successional shifts in vegetation communities and development differences among herb and forb communities relating to competition for light and seedling establishment (Beaudry *et al.* 1997). Low predictability of vegetative species composition is a common phenomenon in early seral SBS stands (Pojar *et al.* 1984) and may partially account for the low similarity in vegetation noted between the two 2yph stands.

Assemblage Ordination

Differentiating separate carabid communities within a successional model (*sensu* Hamilton 1988) based on vegetative characteristic, results in recognition of carabid communities associated with stand disturbance and subsequent recovery (Niemelä *et al.* 1992a,b, Niemelä *et al.* 1993, Atlegrim *et al.* 1997, Koivula *et al.* 2002, Koivula and Niemelä 2003, Heybourn *et al.* 2003). Abundant carabid species can be considered to belong to one of the following groups: forests specialists, forest generalist or open ground species

(Niemelä *et al.* 1993). Koivula (2002), however, suggested a modified model that specifically reflects canopy, which likely better represents the carabid assemblages in a single forest type recovering from disturbance. NMS was selected as the ordination technique for visualization of structures in the community data. While there are weaknesses associated with all ordination techniques (see McCune and Grace 2002), for non-normal, sparse data NMS provides visual representations that adequately re-create patterns that exist in the data with little distortion when compared to detrended canonical correspondence analysis, canonical correspondence analysis or principal components analysis. Carabid groupings observed in NMS (Figure 4) can be interpreted as: a single closed canopy group, a group that does not respond to differences in canopy, and two open or no canopy groups. The clustering in NMS places *Pterostichus riparius* on its own, not associated with canopy influence. This is likely due to *P. riparius* persisting, although declining, through the early successional stages after harvesting, eventually disappearing as canopy develops (Figure 5). Grouping *P. riparius* with *C. advena* and possibly *S. angusticollis* would make sense as all have their highest activity-abundances in closed canopy stands, but *P. riparius* shows a slow decline without recovery in stands developing a canopy, while both *C. advena* and *S. angusticollis* appear to decline after harvest, and then increase again as canopy cover is restored.

Clearcut forest harvesting results in shifts in carabid assemblages, which approximately follow the model proposed by Niemelä *et al.* (1992) (Niemelä *et al.* 1993, Atlegrim *et al.* 1997, Koivula *et al.* 2002, Koivula and Niemelä 2003). Within a single forest type, Koivula's (2002) suggestion to specifically relate carabid communities to cover appears to be more appropriate, however. The general trend in species composition change in

response to disturbance and succession is observed in this study (Figure 4), but the shifts in diversity and activity-abundance differed. Stands with developing canopies had significantly lower diversity than those with open and closed canopies (Table 5), and overall activity-abundance tended to be lower compared to other studies (Niemelä *et al.* 1992a,b, Niemelä *et al.* 1993, Atlegrim *et al.* 1997, Koivula *et al.* 2002, Koivula and Niemelä 2003), which may be in part due to differences in traps (Pearce *et al.* 2005). The general observation of lower carabid diversity in mature stands relative to harvested systems (Niemelä *et al.* 1992a,b, Niemelä *et al.* 1993, Atlegrim *et al.* 1997, Koivula *et al.* 2002, Koivula and Niemelä 2003) was not observed in this study. Alpha diversity in my study area appears to be lower in stands with a recovering tree canopy after harvest when compared to stands with closed or lacking canopies (Table 5). This is in contrast to the findings of Koivula *et al.* (2002), where diversity in stands developing a low canopy was higher due to the presence of "forest-generalist" species, the persistence of "open-ground" species, and the re-establishment of some "forest-specialists".

Studies conducted on the eastern side of the continental divide have found carabid communities that contain at least a few of the same species collected in my study. A few species common in the eastern studies were also relatively common in west central BC. The general assemblage composition of carabids responding to anthropogenic disturbance, and subsequent forest recovery tends to follow patterns observed previously. The group (*sensu* Niemelä *et al.* 1992b) to which an individual species belongs is not necessarily the same, however. For example, Beaudry *et al.* (1997) considered *C. ingratus* and *S. impunctatus* to be forest specialists whereas my data suggest *C. ingratus* to be a species with the greatest abundance under developing canopies. *S. impunctatus*, on the other hand, was most abundant

where canopy development was poor. Neither of these two species was collected in mature stands in my study, and may require higher temperatures than are found in closed canopy stands within the SBS. *Scaphinotus marginatus*, a commonly collected carabid considered a forest specialist in Alberta (Niemelä *et al.* 1993), tended to be collected in all stands suggesting more of a forest generalist distribution in the SBS. Open-habitat specialist, *e.g.*, *Harpalus* and *Amara* species, present in this study were almost absent in young, high elevation regenerating Engelmann spruce - subalpine fir stands (Lemieux and Lindgren 2004), implying that carabid communities in different forest ecosystems respond differently to disturbance, and this may depend both on the proximity to source-populations and on general climatic factors.

Concluding Remarks

My study examined carabid assemblages within the sub-boreal spruce biogeoclimatic zone. Using a forest chronosequence approach I have been able to better understand the dynamics of carabid communities in a single forest ecotype. Within the moist cold variant of the SBS biogeoclimatic zone, carabid assemblage composition, relative abundance and diversity are affected by anthropogenic disturbance, and the subsequent succession of stands. Heybourn *et al.* (2003) suggests that carabid communities, while linked to changing vegetation structures and canopy cover, are influenced by other factors as well. In my study, changes in canopy cover tend to contribute the most influence on carabid activity-abundance and diversity. Variation in vertical vegetation structure, vegetation diversity and ground cover composition also affect carabid assemblages and activity-abundance, as these variables likely influence prey availability and assemblage composition (Vanbergen *et al.* 2007), as well as predation (Brose 2002), competition (Hawes *et al.* 2002), and habitat

selection (Niemelä *et al.* 1994). Variation in sex ratios and implications with regard to habitat quality require further species-specific study before any definitive conclusions can be made.

If not considered, seasonal trends in activity is a factor that can contribute to misleading carabid activity-abundance data in studies that only examine a portion of the snow-free year in temperate climates. The variability of species activity-abundance associated with habitat and season requires the use of caution if carabids are to be utilized in a management context where short sampling windows are implemented.

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Chapter Three

Interactions of *Formica aserva* (Forel), *Camponotus herculeanus* (L.) (Hymenoptera: Formicidae) and carabid beetles (Coleoptera: Carabidae) in sub boreal forests.

Carabid beetles are frequently used as indicator species of habitat change without consideration for the potential influence of other organisms. I examined the interactions of two ant species, *Formica aserva* (Forel) and *Camponotus herculeanus* (L.) (Hymenoptera: Formicidae), and the carabid (Coleoptera: Carabidae) assemblages in different successional stage sub boreal spruce (SBS) stands in west central British Columbia, Canada. A total of 750 Nordlander pitfall traps, in 150 sampling points, were set in 10 stands representing mature, 2 year post harvest (yph), 12 yph, 16 yph and 25 yph. A total of 4801 individual carabids were collected, representing 31 species, over 12 weeks. In stands where carabids co-occurred with *F. aserva* and *C. herculeanus*, non-linear regressions demonstrated a significant effect of *F. aserva* on carabids. Species-specific examination of carabids and ants indicated that *F. aserva* has a generally negative influence on the activity-abundance of carabids, indicating competitive exclusion or predation. The influence of *C. herculeanus* on carabids was also negative, but not as pronounced as that of *F. aserva*, possibly due to lower numbers of *C. herculeanus* or differences in behaviour between the two ant species. An examination of the frequency of injury among several species of carabids revealed a significantly greater frequency in stands dominated by ants than in stands with few or no ants. Pitfall trap-clusters with moderate *F. aserva* activity-abundance had a significantly higher proportion of injured carabids. Trap-clusters with high *F. aserva* activity-abundance had significantly lower carabid activity and lower injury proportions compared to other trap-clusters, probably due to avoidance of ants by carabids coupled with increases in successful

predation of carabids by *F. aserva*. I conclude that carabid activity-abundance and species diversity are influenced by the presence and abundance of ants, particularly *F. aserva*. The influence of *F. aserva* on carabids changes with stand succession, which influence the competitive ability of *F. aserva* colonies.

Introduction

Interactions between ants and carabids are suspected to be important in influencing the distribution, abundance and assemblage composition of carabid beetles (Coleoptera: Carabidae) (Lövei and Sunderland 1996). Based on the observation of a negative correlation between the abundance of carabids and the abundance of red wood ants (Niemelä *et al.* 1992), Lövei and Sunderland (1996) stated that studying carabid communities requires the consideration of ants as a potential factor affecting distribution and abundance. This has been supported by several recent studies (*e.g.*, Koivula *et al.* 1999, Reznikova and Dorosheva 2000, Hawes *et al.* 2002).

Studies examining carabid assemblages and carabids as indicators have generally failed to account for the presence of red wood ants. Lövei and Sunderland (1996) suggest that the results of carabid studies have likely (if not certainly) been influenced by red wood ants, an assertion that is supported by negative correlations between carabids and ants (Niemelä *et al.* 1992, Karhu 1998, Koivula *et al.* 1999, Punttila *et al.* 2004). Many of the observed impacts of ants on carabids stem from research designed to examine the impact of foraging ants on herbivory. For example, Karhu (1998) found a negative impact of *Formica aquilonia* (Yarr.) on carabids in white birch (*Betula pendula*) stands in Finland, and Laakso and Setala (1998, 2000) indicated that predatory invertebrate mesofauna, which include carabids, significantly increased in activity-abundance with the removal of *F. aquilonia*

nests. Punttila *et al.* (2004) found that red wood ants impacted carabid abundance at elevations where they were both present in birch (*Betula* spp.) forests in Finland. Mody and Linsenmair (2004) noted that exclusion of three species of *Camponotus* ants from trees in the Republic of Cote d'Ivoire (West Africa) resulted in an increase in arboreal carabids. Studies examining carabid distribution, as it relates to habitat in natural and disturbed systems, have also led to observations of negative carabid-ant associations; for example, Niemelä *et al.* 1992 found mostly negative associations between the pitfall catches of carabids and red wood ants in coniferous Finnish forests. Carabid abundance was also negatively influenced by the presence of red wood ants in post-harvest stands in Finland (Koivula 2002). Furthermore, Koivula *et al.* (1999) found a significant negative impact of red wood ants on carabids while examining the effect of leaf litter on carabid abundance, as did Koivula and Niemelä (2003) when examining the impact of harvesting prescriptions on carabids. Studies examining biodiversity and the use of invertebrates as indicator taxa have uncovered negative associations between carabids and wood ants as well. For example, Oliver and Beattie (1996) found a strong negative correlation between ants and both carabid and scarab beetle species richness in Australian forests. Foord *et al.* (2003) noted a negative association between carabids and wood ants in South Africa.

Studies designed to specifically examining the relationship between carabids and ants are limited to two. Reznikova and Dorosheva (2004) examined behavioural responses of carabids in the presence of *Formica polyctena* (Foerst.), a Eurasian species of red wood ant. Carabids demonstrated a host of species-specific responses to the presence of red wood ants, and the presence of *F. polyctena* influenced the spatial distribution of all carabid species examined. Hawes *et al.* (2002) found that red wood ants significantly affected carabid

activity-abundance in a Scots pine plantation in England, more so than variation in vegetation. The impacts differed among carabids of different size-classes and between sexes of the most abundant carabid species, *Abax parallelepipedus* (Piller & Mitterpacher).

Vegetation species composition, stand vertical structure and field vegetation characteristics (*e.g.* density, vigour, vegetation colour)tend to reflect variation in moisture, nutrients and light penetration. These variables tend to be intertwined and affect carabids in manners that differ, depending on landscape level variables such as degree of fragmentation, elevation, the geographic location and disturbance history (Ribera *et al.* 2001). Conversely, the influence exerted by the presence of aggressive ants on carabids has been negative in all studies to date.

Ants tend to form dominance hierarchies in multi-ant-species communities, with the largest colonies and the most dominant ant species benefiting from interference competition (Fellers 1987, Savolainen and Vepsäläinen 1988, Hölldobler and Wilson 1990). Many of the competitive relationships among different ant species are affected by forest canopy removal, and shifts in environmental conditions (Punttila *et al.* 1994, 1996). Temperature influences the ant assemblage and different foraging and behaviours are exhibited by differing species, with behaviourally aggressive species often having a narrower thermal tolerance than species with broader tolerances (Lessard *et al.* 2009).

Pitfall trapping is useful in examining the activity-abundance of both carabids (Spence and Niemelä 1994) and ants (Melbourne 1999). This manner of collection, however, is poor at showing evidence of physical interactions between organisms. To be able to glean additional information pertaining to the interactions between organisms from pitfall trapping, a closer examination of trapped organisms for injuries may reveal some

information about their past interactions. Observation of injuries to infer deleterious interactions has been used in studies examining intra-specific aggression in howler monkeys (*Alouatta palliata mexicana*) (Cristóbal-Azkarate *et al.* 2004), and sexual competition among male fig wasps (*Philotrypesis pilosa*) (Murray 1987).

The use of injuries to infer predation pressure has been used in studies of both vertebrates and invertebrates. Use of limb loss to infer aggressive interactions or failed predation attempt has been used for jumping spiders (Taylor and Jackson 2003) as well as in other species that use autotomy to avoid predation (Magginis 2006). Autotomus injuries are consistent within species and occur along a fracture plane. These types of injuries do not appear to occur in adult carabids (Magginis 2006), and evidence of predation of adult carabids by ants is sparse. Interactions other than predation, e.g., interference competition, may result in injuries as well. Studies examining interference in ant communities have shown biting to be a dominant form of aggression in *Camponotus* and *Formica* ants (Fellers 1987), leading to the hypothesis that injuries to carabids could be caused by encounters with aggressive ants. In my study area, *Formica aserva* (Forel) and *Camponotus herculeanus* (L.) are the most likely species to influence the carabid assemblage, as they represent the numerically dominant species in regenerating stands (R.J. Higgins[1], pers. comm.).

The objectives of this study are: to examine the relationship of two abundant species of ants, *Formica aserva* and *Camponotus herculeanus*, on carabid activity-abundance; to examine carabid assemblage composition in relation to these ants in stands with varying canopy closure; and to examine the interactions between dominant ants and carabid injury to infer possible interference competition and/or predation.

[1] Assistant Professor, Thompson Rivers University, Williams Lake, BC.

Methods

Study Sites

The study was conducted in the same ten stands (study sites) as described in Chapter 2 within the operating area of West Fraser's Houston Forest Products Division (HFP West Fraser). Sites were restricted to lodgepole pine-leading stands within the sub boreal spruce biogeoclimatic zone (SBS). This biogeoclimatic zone generally occurs between 800 m to 1300 m above sea level in central British Columbia (between latitudes 51° 30' and 59° N). Mean annual temperatures range between 1.5°C and 5°C, with 2-5 months having average temperatures below 0°C. *Picea glauca* (Moench) Voss x *Picea engelmanni* Parry ex Engelm. and *Abies lasiocarpa* (Hook.) Nutt. are the dominant climax tree species, with *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm a common seral species (Meidinger and Pojar 1991). Two sites were chosen in each of the following post harvest age classes: 2 years post harvest (yph), 12 yph, 16 yph, >25 yph and non-harvested to represent successional shifts in vegetation structure from open ground to low canopy, and a gradient ranging from no canopy (0% coverage) to closed canopy (100% coverage). Within each site, a one hectare sampling plot was randomly positioned at least 50m away from an edge (*i.e.*, road, stream, abrupt elevation change, forest or cutblock edge). The exact study site locations are listed in Appendix I.

Pitfall Sampling

Trap-clusters were placed within sites to avoid inclusion of any feature that would exclude trapping, *e.g.*, anthropogenic structures and wet areas. Each of three 80m long transects running at randomly determined bearings from randomly selected points of commencement within the plots, and not constrained by the plot boundary, were established.

Traps were established as described in Chapter 2 (Chapter 2, Figure 1) with trapping clusters separated by a minimum of 14m.

Modified Nordlander pitfall traps (Lemieux and Lindgren 1999) as described in Chapter 2 were filled with 90mL of 25% propylene glycol solution in water. Samples were collected and the fluid replaced every 14 days from May 25, 2005 until August 28, 2005. Captured carabids were processed as described in Chapter 2. Carabids and ants from each individual pitfall trap were identified (see below) and then placed in labelled vials containing 70% ethanol. Several specimens from each species; a minimum of 10 where possible, were pinned and labelled. Voucher specimens have been deposited at the Strickland Entomological Museum, University of Alberta, Edmonton, Alberta, and the Royal BC Museum, Victoria, British Columbia.

Following identification and sexing, carabids were examined for physical deformities and injuries (*e.g.,* amputation of extremities, cuts or breaks in elytra, abnormal fusing of body or limb/antennae segments). Injuries were determined to be pre-collection if they showed evidence of sclerotization (*i.e.*, healing) (Figures 6 & 7). Carabids with injuries showing no sclerotization, or where determination of sclerotization was impossible, were tallied as uninjured. As carabids tend to move and search for food using a random walk pattern (Wallin and Ekbom 1994), a significantly higher frequency of injuries at higher activity-abundances could be the result of intra-specific or inter-specific encounters. If the majority of injuries inflicted on conspecifics occur in contests for mates, it is reasonable to assume that males competing for mates would have a higher proportion of injuries than females of the same species.

Specimen Identification and Data Collection

Carabids were identified according to Lindroth (1961-1969) and sexed. Confirmation of species identification was undertaken at the Canadian Forest Service, Northern Forestry Centre, and the Strickland Entomological Museum, University of Alberta, both in Edmonton, Alberta. *Camponotus* and *Formica* ants were identified to species using Wheeler and Wheeler (1963, 1986) and Naumann *et al.* (1999).

Carabid and ant data were standardized to 100 trap-days prior to analysis. Standardization was the sum of the five traps in each trapping cluster divided by total number of days the trap-cluster was operational multiplied by 100. Missing, destroyed, or damaged traps for each cluster were accounted for by multiplying the summed total of the trap cluster by 1, plus 0.2 for each missing, damaged or destroyed trap. This reduced the comparative influence of lower trap days for traps that were destroyed, damaged or otherwise disturbed during a 14 day sample period.

Formica aserva and *C. herculeanus* activity-abundances were then categorized. Activity-abundance of *F. aserva* at each trap-cluster was assigned to one of four categories based on the standardized activity-abundance at the trap-cluster. Categories were as follows: Absent - *F. aserva* were not observed at the trap-cluster, Low - between 1 and 50 workers were collected at the trap-cluster, Moderate - between 51 and 150 workers were collected at the trap-cluster and High - more than 150 workers were collected at the trap-cluster. *F. aserva* colonies in the SBS do not occur in mature stands or young post-harvest stands (Higgins 2010), thus trap-cluster occurring in mature and 2 yph stands were excluded from analysis. *Camponotus herculeanus* activity-abundances at the trap-cluster were similarly categorized into four groups. The ratio of *C. herculeanus* to *F. aserva* (0.225:1) was used to

generate *C. herculeanus* activity-abundance categories proportionally similar to those of *F. aserva.* Thus, *C. herculeanus* activity-abundance was categorized as: Absent - *C. herculeanus* were not observed at the trap-cluster, Low - between 1 and 11 workers were collected at the trap-cluster, Moderate - between 12 and 34 workers were collected at the trap-cluster and High - more than 34 workers were collected at the trap-cluster.

Data Analyses

Statistical analyses were preformed using SYSTAT 11 (Systat Software, Inc., Chicago, IL) except where otherwise noted.

Non-linear regressions were used to examine the effect of *F. aserva* on *C. herculeanus*, on carabid activity-abundance (Sigmaplot v.11). Environmental effects were limited by truncating the data set including in the analyses only stands where *F. aserva*, *C. herculeanus* and carabids occurred, *i.e.*, 12, 16, and 25 years post harvest (yph). ANOVA was used to examine the effect of *F. aserva* activity-abundance groups on carabids activity-abundance. The truncated carabid activity-abundance was square root transformed prior to analysis. Where one-tailed ANOVAs were significant, post-hoc examination using Tukey's correction were performed.

Carabid injury data were evaluated for all sites and stand ages, and then truncated as above prior to ANOVA to examine the influence of ants on injury proportions.

Data plots of carabid and ant activity-abundance at the trap-cluster were used to visualize the relationship between carabids and ants in stands where they co-occurred. Species that accounted for at least 2% of the total carabid catch were examined individually. Trap-cluster by trap-cluster activity-abundance of all carabids, *F. aserva*, and *C. herculeanus* was constructed to examine the interrelationship among all species.

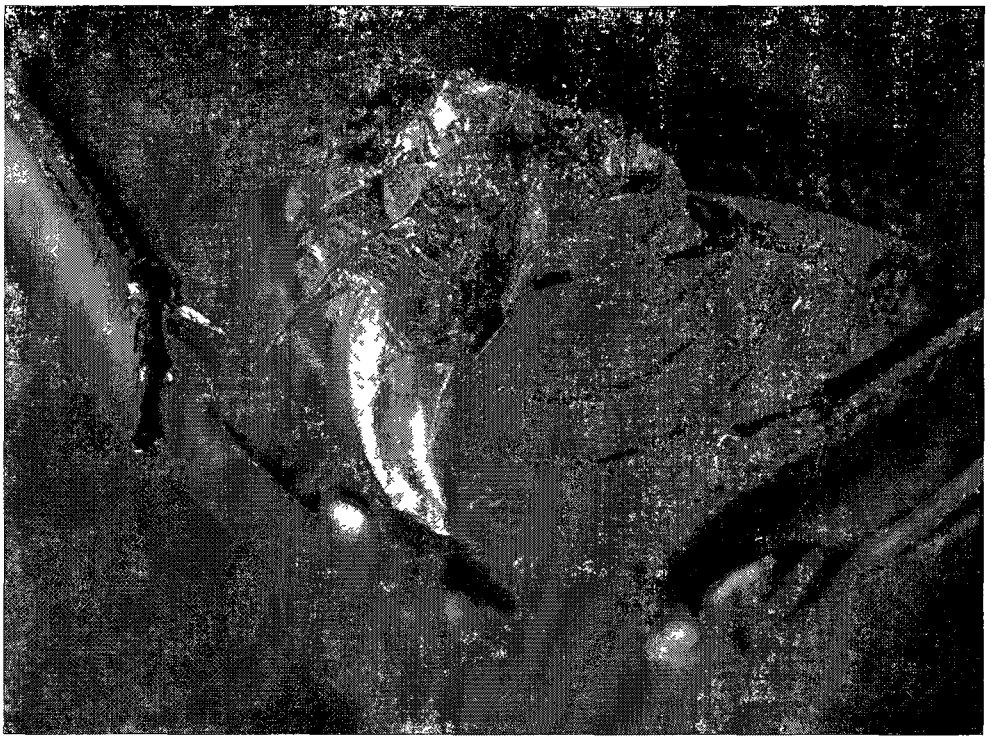

Figure 6: ***Scaphinotus marginatus*** **with injured tarsus (left)** ***vs.*** **broken tarsus (right). Photo: Ward B. Strong**

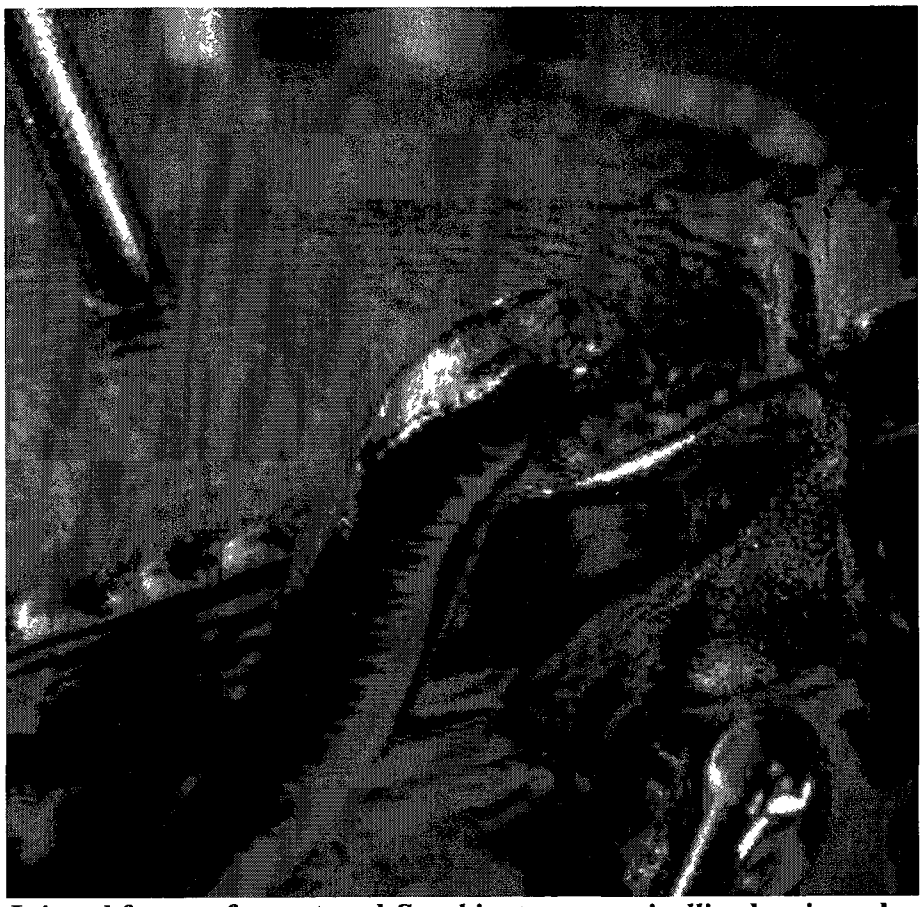

Figure 7: Injured femur of a captured *Scaphinotus angusticollis*, showing sclerotization at the severed end. Photo: Ward B. Strong

Carabids with injuries were tallied, and frequencies of occurrence were determined for each species, gender and stand age. Observed frequencies of injury were then compared, using Chi squared tests, against expected injury frequencies.

Injury proportions were calculated for each of the four *F. aserva* and *C. herculeanus* activity-abundance categories. Proportional data were then transformed as $x' = \log10 (x + 0.01)$ to achieve a normal distribution. Carabid injury proportions, grouped by *F. aserva* and *C. herculeanus* activity-abundance categories, respectively, were examined using ANOVA. For *C. herculeanus*, *F. aserva* activity-abundance was used as a covariate to account for its effect on carabids injury proportions.

Results

Ants and Carabids

Residual plots indicated that the relationship between carabids and *F. aserva* is curvilinear in form. Comparison of residual standard deviations and standard deviations of the data set indicated that the non-linear regression fit to a decay curve was a better fit than the linear form as did regressions examining the relationship between *C. herculeanus* and *F. aserva*. Non-linear regression showed a significant effect of *F. aserva* activity-abundance on carabid activity-abundance (Figure 8), although only 16.5% of the variation was explained by *F. aserva* activity-abundance. All of the regression coefficients were significant (α = 0.05).

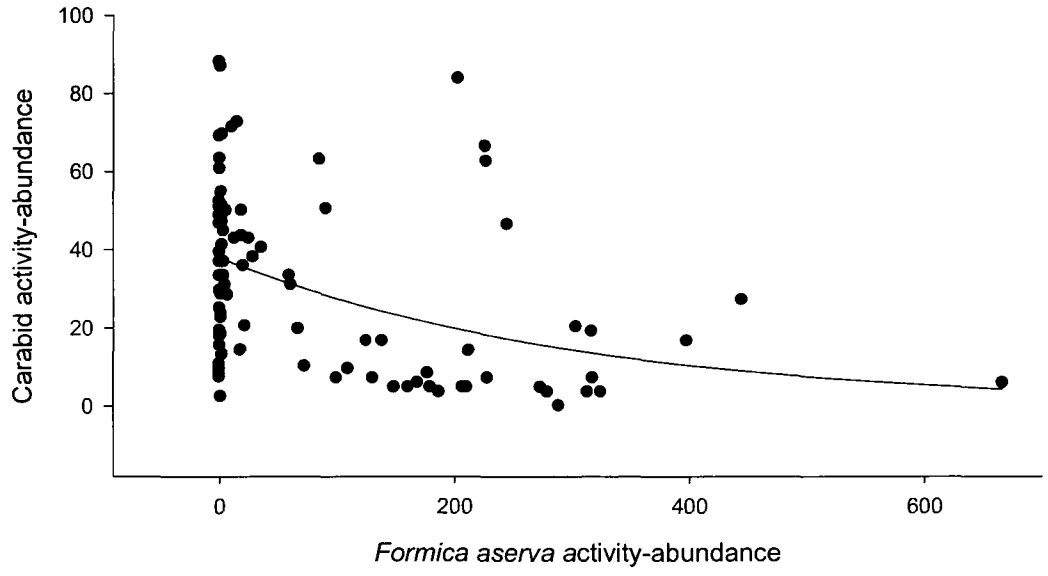

Figure 8: Non-linear regression of carabid activity-abundance predicted by the ant *Formica aserva* y = 37.9587*exp(-0.0032*x); Adjusted R^2 = 0.165; F = 17.439; P < 0.0001.

There was no significant influence of *C. herculeanus* activity-abundance on carabid activity-abundance (P = 0.081) examined using non-linear regression. Activity –abundance

of *C. herculeanus*, however, shows a negative and curvilinear relationship with the activity-abundance of *F. aserva* (Figure 9). These data failed to improve with transformation and thus failed tests for normality and homoscedasticity.

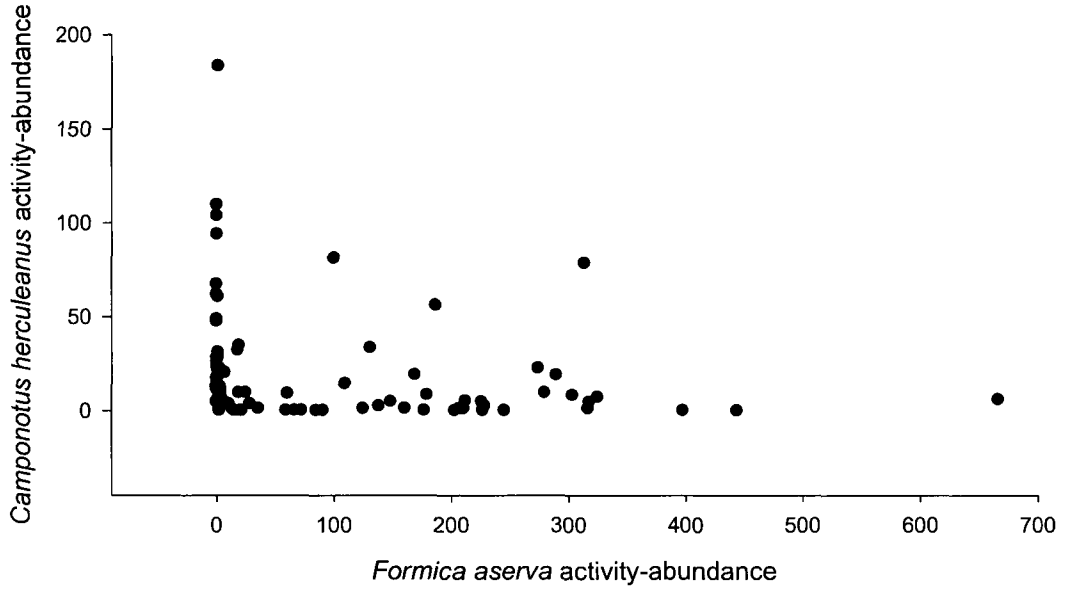

Figure 9: Plot of *Camponotus herculeanus* activity-abundance against *Formica aserva* activity-abundance showing a negative association between the two species.

Non-linear regression of *F. aserva* and *C. herculeanus* activity-abundance, respectively, with individual common carabid species failed to produce significant results due to low R^2 values and/or high Predicted Residual Error Sum of Squares (PRESS) values, indicating low predictive value of the models. Carabid and ant distributions, in nearly all cases, tend to be what McCune and Grace (2002) describe as a "dust bunny distribution", *i.e.*, data points cluster along the axes with a tendency for a cluster of points near the origin, indicating avoidance. , howeverFor most common carabid species the dust bunny distribution is much stronger for *F. aserva* than for *C. herculeanus* (Figure 10 a-i), except *T. chalybeus* (Figure 10 j).

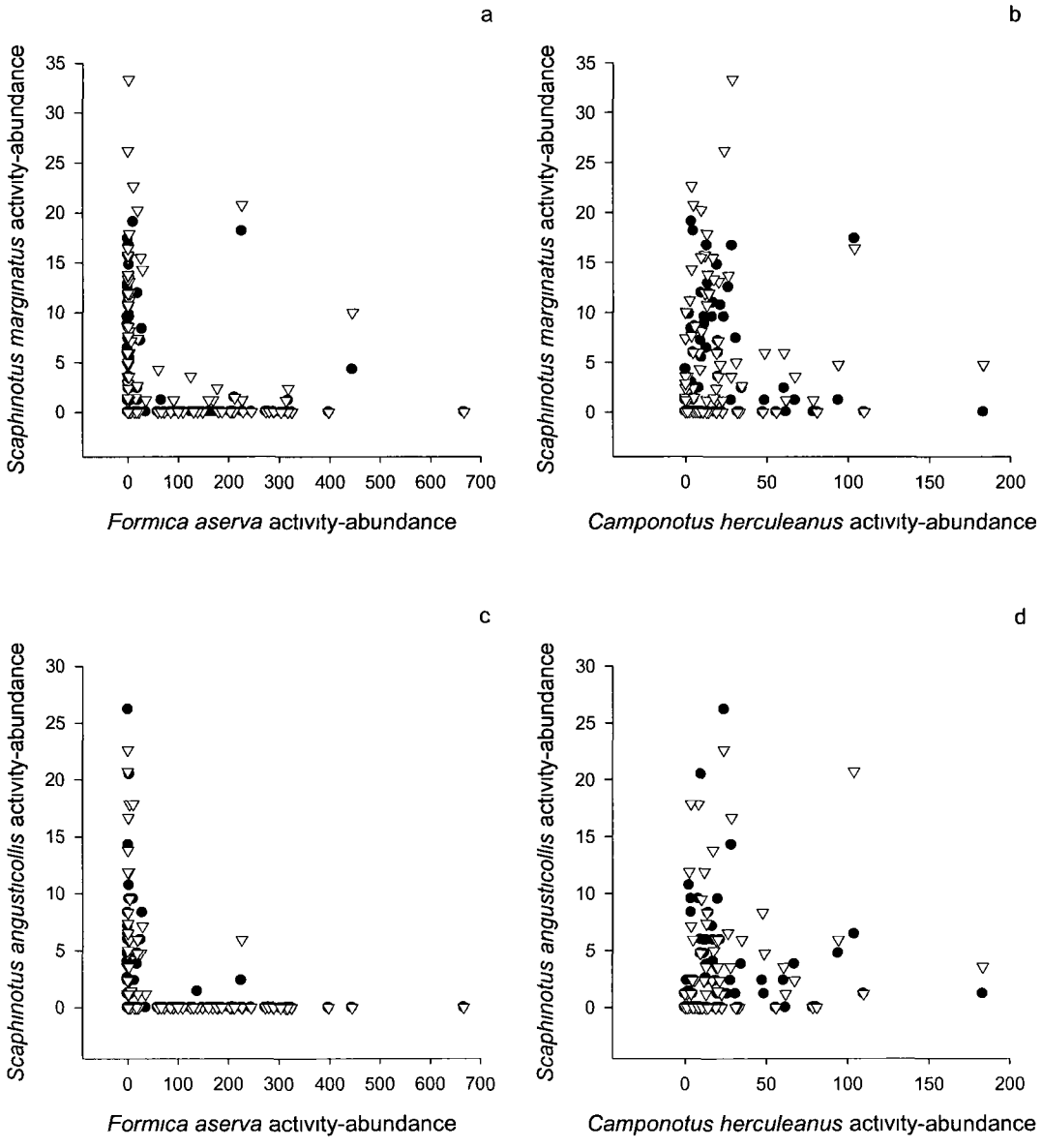

Figure 10. a-d: Carabid activity-abundance in mid-successional sub boreal spruce stands plotted against *Formica aserva* (a, c) or *Camponotus herculeanus* (b, d) activity-abundance. Male carabids: ▽, Female carabids ●

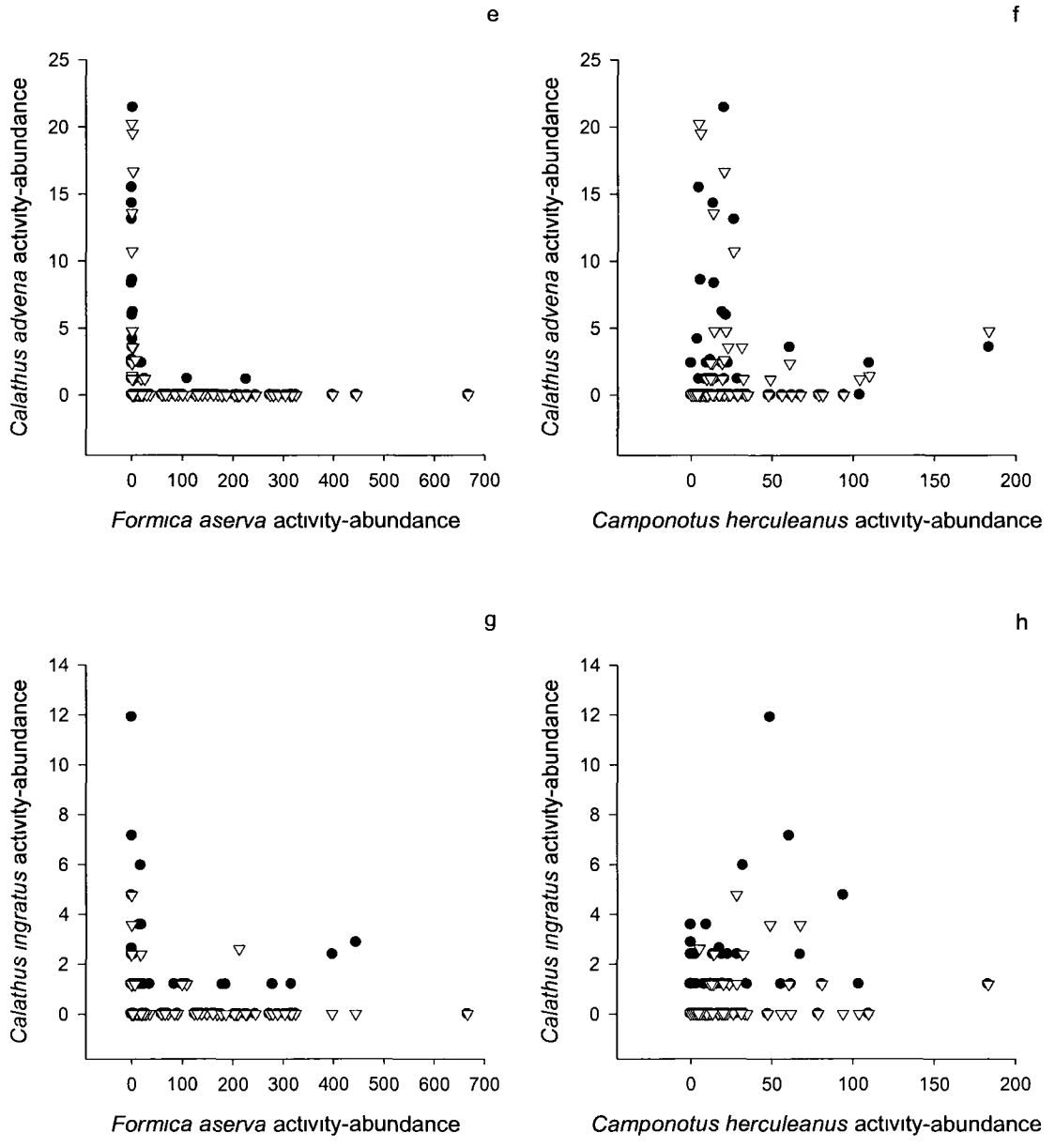

Figure 10 continued. e-h: Carabid activity-abundance in mid-successional sub boreal spruce stands plotted against *Formica aserva* (e, g) or *Camponotus herculeanus* (f, h) activity-abundance. Male carabids: ▽, Female carabids ●

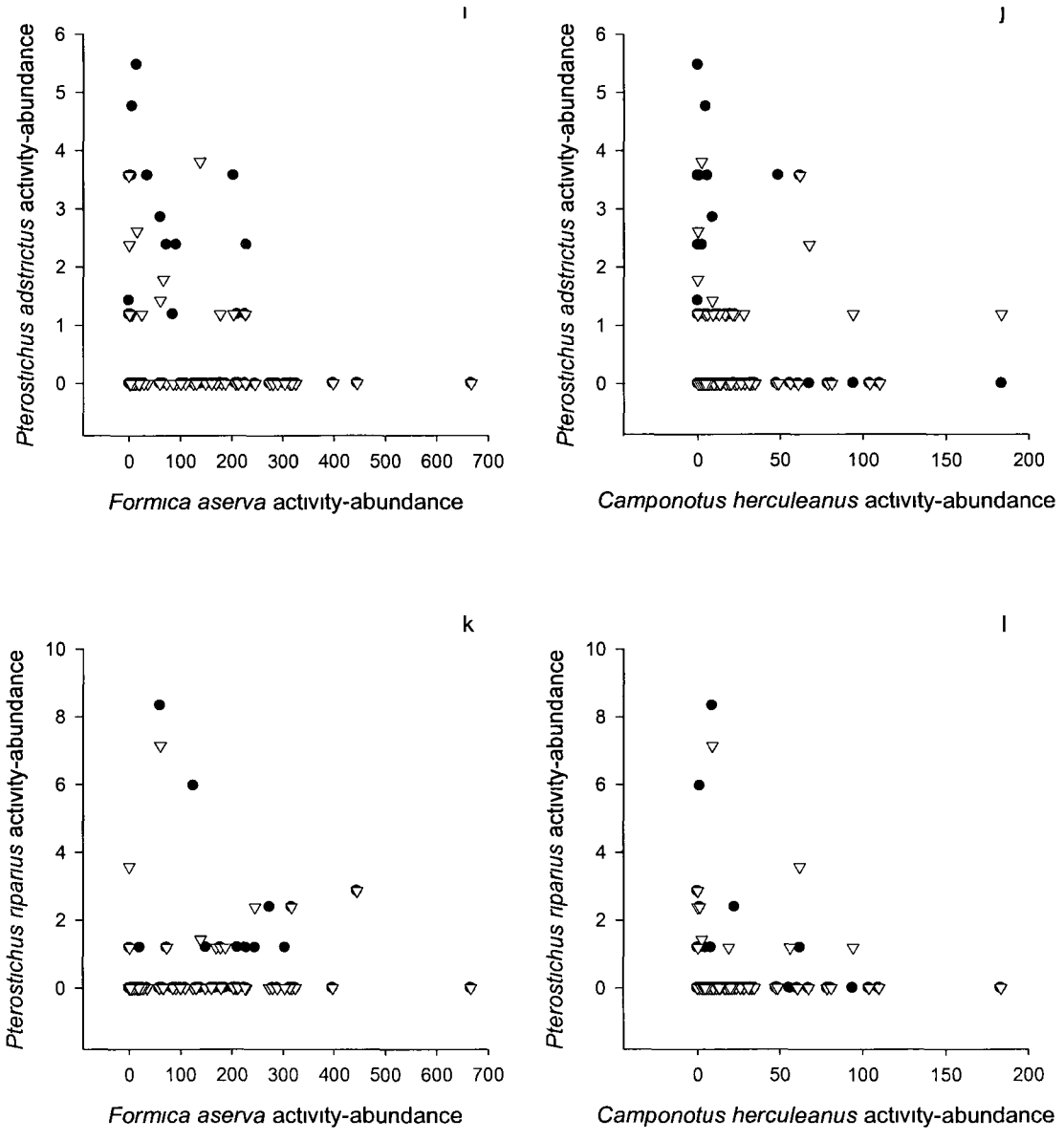

Figure 10 continued. i-l: Carabid activity-abundance in mid successional sub boreal spruce stands plotted against *Formica aserva* (i, l) or *Camponotus herculeanus* (j, l). Male carabids: ▽, Female carabids ●

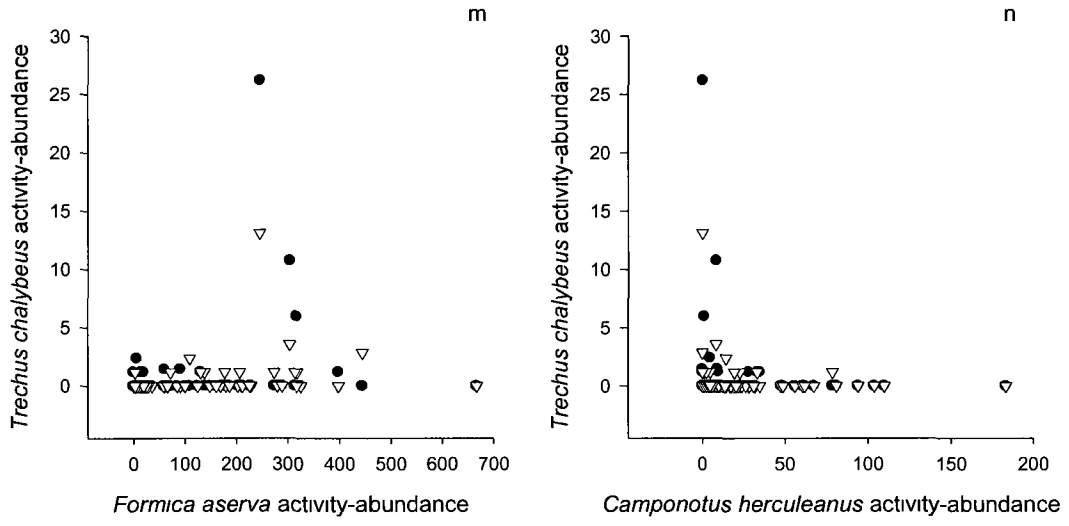

Figure 10 continued. m & n: Carabid activity-abundance in mid successional sub boreal spruce stands plotted against *Formica aserva* (p) or *Camponotus herculeanus* (m) activity-abundance. Male carabids: ▽, Female carabids ●

ANOVA showed a significant impact of *F. aserva* on carabid activity-abundance ($F_{(3,86)} = 9.15$; $P < 0.001$), and *a posteriori* tests showed that trap-clusters with no or low *F. aserva* activity-abundance had significantly higher carabid activity-abundance than trap-clusters with moderate or high *F. aserva* activity-abundance (Figure 11).

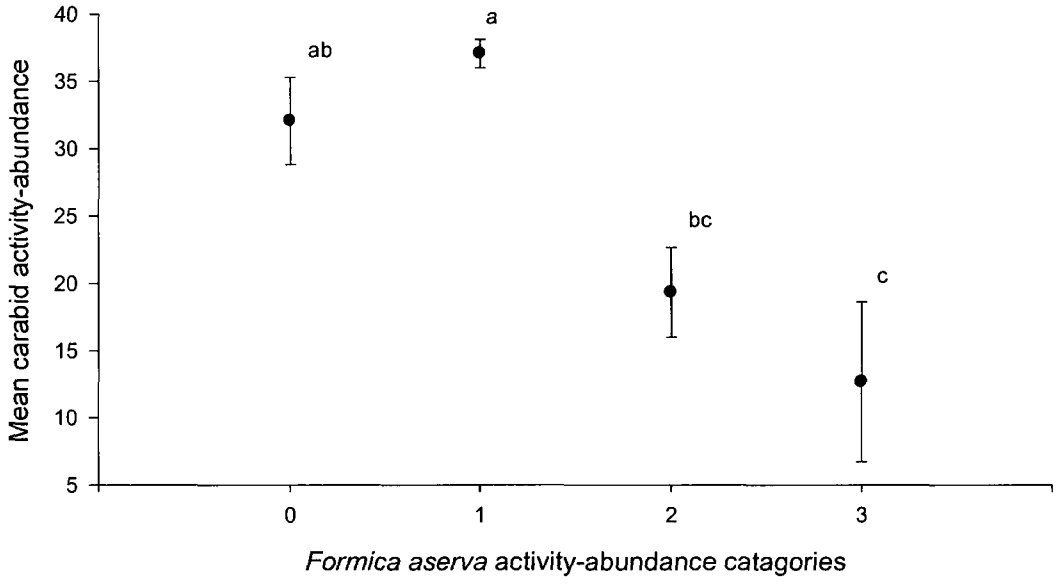

Figure 11: Relationship between mean (±SEM)activity-abundance of carabids and activity-abundance *Formica aserva*: Absent (0) – *F. aserva* were not observed at the plot, Low (1) - between 1 and 50 workers were collected at the plot, Moderate (2) - between 51 and 150 workers were collected at the plot and High (3) – more than 150 workers were collected at the plot. Means with the same letter designations are not significantly different as determined by Tukey's tests.

Injury

A total of 774 carabids, 16.12% of the total catch, possessed some damage that was categorized as pre-capture injury. For most common carabid species significant stand age associated differences in frequency of injury were observed (Table 3).

Table 3: Summary of χ^2 analysis on injury frequency of carabids in stands before and at different successional stages after harvest[1] (yph = years post harvest). ($\chi^2_{crit} = 3.841$: df =1; $\alpha = 0.05$ for all tests; Significant χ^2 results values are given)

	Successional stage				
Species	**2 yph**	**12 yph**	**16 yph**	**25 yph**	**Mature**
Scaphinotus angusticollis	0	0*	0	+ + + 17.432	- - - 24.628
Scaphinotus marginatus	- 4.795	- 5.543	+ 8.197	0	0
Pterostichus adstrictus	0	0	+ + 6.807	0	0
Pterostichus riparius	0	0	0	n/a	0
Calathus advena	0*	0*	+ + 7.856	+ 5.795	0
Calathus ingratus	n/a	0	0	0	n/a
Synuchus impunctatus	- 4.609	0	0	0	n/a
Trechus chalybeus	- - 7.138	+ 5.838	+ + + 23.190	0*	0

[1]"-" significantly fewer ($P < 0.05$)
"- -" significantly fewer ($P < 0.005$)
"- - -" significantly fewer ($P < 0.001$)
"+" significantly more ($P < 0.05$)
"+ +" significantly more ($P < 0.005$)
"+ + +" significantly more ($P < 0.001$)
* low sample size n < 10

Proportions of injured carabids per trap-cluster differed significantly with *F. aserva* activity-abundance category ($F_{(3, 86)} = 3.215$; $P = 0.027$) with the significantly greatest proportion of injured carabids at moderate *F. aserva* activity and the fewest at high *F. aserva* activity. *C. herculeanus* activity-abundance did not significantly affect carabid injury proportions ($F_{(3, 85)} = 1.738$; $P = 0.165$), although the proportion of injured carabids was lowest at moderate *C. herculeanus* activity.

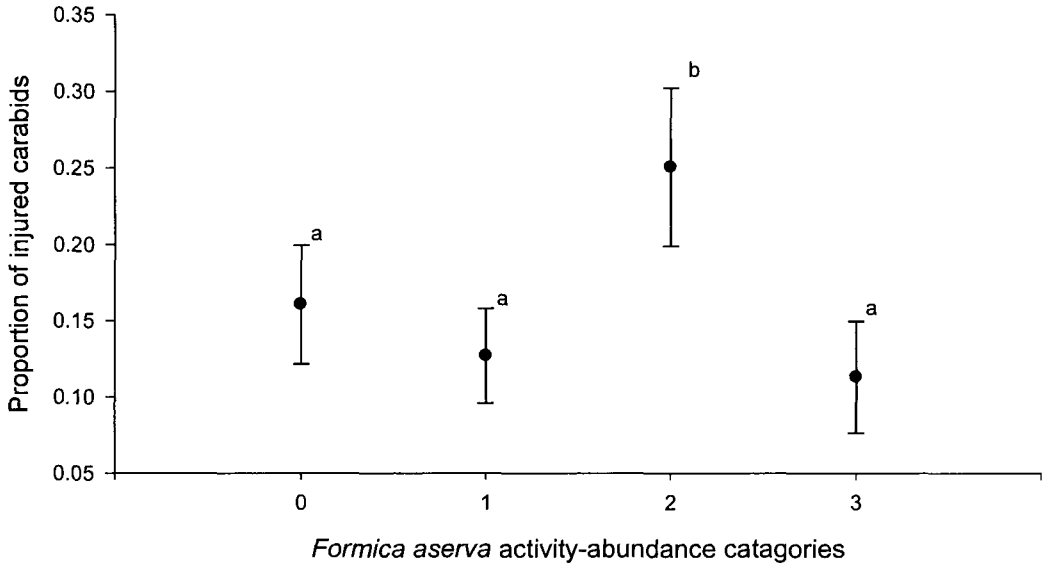

Figure 12: Relationship between proportion of injured carabids (±SEM) and activity-abundance of *Formica aserva*: Absent (0) – *F. aserva* were not observed at the plot, Low (1) - between 1 and 50 workers were collected at the plot, Moderate (2) - between 51 and 150 workers were collected at the plot and High (3) – more than 150 workers were collected at the plot. Means with the same letter designations are not significantly different as determined by a posteriori Tukey's tests.

Discussion

Assemblage structure can be attributed in part to competitive interactions (*e.g.*, Morse 1970), and has been shown to be important in structuring ant communities (Punttila *et al.* 1994). Inter-guild predation, *i.e.,* predation between species that occupy similar niches, on carabid larvae has been demonstrated experimentally, and may play a role in carabid communities (Currie *et al.* 1996). Competition among carabid species in the absence of other ground-dwelling invertebrates has been viewed as minor for structuring carabid assemblages based on adult carabid data, however (Lövei and Sunderland 1996).

While not directly examined, morphological differences among species of carabids reflect differing ecological functions and specific adaptations that likely influence habitat selection (Forsythe 1987) and niche differentiation (Loreau 1988). As forests recover from anthropogenic disturbance, competitive abilities of epigaeic invertebrates influenced by stand structure can shift. Competitive shifts likely influence the ability of carabids to occupy habitats and possibly manifest as observed shifts in activity-abundance (see Chapter 2) or changes in dominance hierarchies. Shifts in competitive ability have been observed for ants (Punttila *et al.* 1994) and in carabids (Niemelä *et al.* 1993) in stands recovering from disturbance.

The trend towards lower carabid activity-abundance in stands with established ant colonies has been observed in numerous studies (Niemelä *et al.* 1992, Oliver and Beattie 1996, Karhu 1998, Laakso and Setala 1998, Koivula *et al.* 1999, Laakso and Setala 2000, Hawes *et al.* 2002, Koivula 2002, Foord *et al.* 2003, Koivula and Niemelä 2003, Mody and Linsenmair 2004 (*Camponotus* species), Punttila *et al.* 2004, Reznikova and Dorosheva 2004). Observations of increased activity-abundance of carabids with relatively low ant activity-abundance (Figure 11) may indicate that a threshold of ant activity must be reached before a decrease in carabid activity-abundance results. This pattern may be an artefact of carabids modifying their behaviour, *e.g.* increased movement (Reznikova and Dorosheva 2004) in the presence of potential threats (*e.g.*, *F. aserva*), as opposed to an increase in the number of carabids present *per se*. Clustering of data points along axes in plots of carabid versus ant activity abundance (Figure 10) indicates an aversion between most abundant carabids and *F. aserva*, and to a much lesser degree between some species of carabids and *C. herculeanus*. Innate aversion of ants is thought to exist in some jumping spider species

(Nelson and Jackson. 2006), but may be a learned response in predominantly insectivorous carabids. Learned avoidance does not seem to occur as readily, if at all, in seed predators (Reznikova and Dorosheva 2002). Avoidance may not be universal as some species may be keying in on ant colonies as a potential food source (Kolbe 1969 cited in Reznikova and Dorosheva 2004). Thus response of carabids to the presence of ants is not necessarily similar between species, which likely contributes to the high variation observed in tests examining the carabid assemblages a whole and *F. aserva*.

While not a member of the red wood ants (*Formica rufa* group), aggressive behaviour of *F. aserva* is likely similar to what has been observed in other dominant ant species (Savolainen *et al.* 1989, Punttila *et al.* 1994), and may result in avoidance behaviours by other invertebrates. Such avoidance behaviour has been observed in carabid and spider interactions with ants (Reznikova and Dorosheva 2004, Nelson and Jackson. 2006) and is suggested by negative regression values for both carabids and *C. herculeanus* relative to *F. aserva.*

Generally when ants encounter a potential prey item the initial physical encounter involves the seizing of prey appendages with its mandibles (personal observation). Similar species of ants show aggression in the form of biting (Fellers 1987), and it is quite likely that physical interactions between carabids and *F. aserva* or *C. herculeanus* result in deleterious impacts on the injured carabid such as loss of limb segments. Carabids may attempt to avoid this type of physical interaction with formicine ants (specifically ants in the *Formica rufa* group) to protect their appendages (Reznikova and Dorosheva 2004).

Variation in the frequency of injury among carabid species suggests different competitive relationships among predatory epigaeic invertebrates in different successional

stands. If observed injuries were the result of carabids competing with carabids, both inter- and intra- specifically, then trends in injury frequency when examined without consideration of *F. aserva* fit the hypothesis that competition among carabids does not play a role in structuring their communities, a conclusion also suggested by Loreau (1988). It is unlikely that the injuries observed in carabids were the result of sexual competition as variation in frequency of injury among males and females within the most abundant species was not significant. The possibility that injuries observed in carabids are the result of interactions among carabids is also unlikely, as in stands with high carabid activity-abundance observed injury frequencies were significantly lower than expected, or no different than those in stands with the low carabid activity-abundance. For example *S. angusticollis* (Table 4) mean activity-abundance in mature and 25 yph stands did not differ significantly, but observed injury frequency was higher than expected in the 25yph stand, but significantly lower in the mature stand, indicating carabid injury frequency is not dependant on activity-abundance, especially for *S. angusticollis*.

Significantly higher than expected carabid injury frequencies were observed (summarized in Table 4) where ants, particularly *F. aserva*, appear to be the dominant epigaeic predator, while lower than expected injury frequencies occurred in stands without of with few or no ants present. Interaction with the aggressive *F. aserva* resulted in fewer carabids being present where the activity-abundance of this ant is high, and a greater proportion of those carabids present possess some form of injury. This relationship was not observed between carabids and *C. herculeanus*, although it is possible that the relatively low activity –abundance for *C. herculeanus*, in comparison to *F. aserva*, may mask their interactions with carabids.

Schoener (1979) developed a model for relating frequency of injury of lizards to predation pressure. He determined that if predation (by the assumed predator) is the primary cause of mortality then decreased injury frequencies indicate increased predation pressure. Subsequent studies have demonstrated that high injury frequencies also indicate inefficient predation (*e.g.* Medel *et al.* 1988). For the ant-carabid system I examined, Schoener's (1979) model likely is inappropriate as predation by ants is unlikely to be the primary agent of mortality, and injuries are not likely to be an evolutionary escape mechanism (autotomy) as seen in many lizards. The predators (ants) in my study are social, so predation efficiency is in part a function of colony size, location, and recruitment ability. Thus, a proportion of the injuries observed in carabids may be due to interference rather than predation. My results show a positive density effect of *F. aserva* on carabids (Figure 11); at low ant activity-abundance level fewer carabids are collected suggesting avoidance. At moderate ant activity-abundance levels, the interaction between carabids and *F. aserva* may manifest as interference or failed predation attempts, resulting in an increase in injury frequency. At high ant activity-abundance, *F. aserva* is able to recruit a sufficient force rapidly enough for successful predation (decrease in injury) (Figure 12).

The differences in influence exerted on carabid assemblages by *C. herculeanus* and *F. aserva* may be due to behavioural differences between the two ant species, as *Formica* have been shown to be more territorial and aggressive than *Camponotus* in Europe (Savolainen and Vepsäläinen 1988).

Complex interplay between stand structure, competitive abilities, assemblage composition and activity-abundance can all be inferred from the data presented here. Acknowledging the possibility of multiple interactions within the epigaeic arthropod

community is necessary if advancement in our understanding of forest arthropods is to be achieved. The knowledge that ants may influence the behaviour, distribution, species composition and diversity of carabid assemblages (Hawes *et al.* 2002, Reznikova and Dorosheva 2004), needs to be integrated into studies examining carabid beetles. Integration is particularly needed where managers seek to monitor forest invertebrates, where the relative influence of ants on carabid assemblages vary as carabid and ant assemblages shift as stand succession proceeds.

The level of ant activity-abundance needed to elicit effects on carabid injury frequency and carabid activity-abundance are influenced by the environment, carabid assemblage composition, and the dominant species of ant. Since the effect of ants on carabids is density dependant, and ant densities can vary greatly by species and are also dependent on environmental variation (Hölldobler and Wilson 1990), the effect that ants have on carabid communities will likely differ somewhat based on species composition and species-specific adaptation to avoiding ants (Reznikova and Dorosheva 2004). Therefore, prior to drawing broad conclusions across ecosystems and community composition based on the levels of activity presented here, further examination of interactions within epigaeic invertebrate communities that have an aggressive resident ant population are needed.

While this study showed interactions between carabids, *F. aserva* and *C. herculeanus*, additional studies of mechanisms, identification of the resources subject to competition, and of various invertebrate interactions are needed to understand the dynamics of the epigaeic predatory arthropod community.

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Chapter Four

Effect of addition of *Formica aserva* (Forel) (Hymenoptera: Formicidae) nests on a carabid (Coleoptera: Carabidae) assemblage

Evaluation of carabids (Coleoptera: Carabidae) as indicators of forest ecosystem health has largely ignored the influence of ants (Hymenoptera: Formicidae) on carabid distribution, abundance, diversity, assemblage composition, and behaviour. To examine the influence of *Formica aserva* (L.), a dominant aggressive ant, on carabids, *F. aserva* nests were added to a clearcut stand where it was absent.

A significant effect of distance from plot center on the activity-abundance of carabids was detected. This effect was possibly influenced by colony "choice" and viability in the ant treatment. Behavioural response of carabids in the presence of ants (increased movement) and as a result of variation in habitat quality, as well as trap interaction at the 0.5m distance from the treatment may also have influenced this result. No significant treatment effects were found for individual carabid species, however. Possible explanations for the weak experimental results and the subsequent difficulties in interpretation may be due to trapping depletion due interaction between 0.5m traps, influence of habitat patch differences between the treatments and control, differences in colony size and persistence over the experiment, and issues with colony transplanting. Loss of foragers and difficulties in ensuring the presence of a queen made establishment success of transplanted colonies poor. Nevertheless, this study indicates that accounting for interactions between carabids and ants may be valuable in the development and implementation of models using carabids as indicators.

Introduction

Interference competition is suggested to explain interactions between ants (Hymenoptera: Formicidae) of different species. For example, *Formica polyctena* Foerster (a Eurasian red wood ant) affected prey retrieval and selection in *Formica fusca* L. (Savolainen 1991), and *Leptothorax* sp. and *Lasius flavus* (F.) nest numbers increased following the decline of *Lasius niger* (L.), which in turn resulted from the introduction of the red wood ant *Formica truncorum* (F.) (Rosengren 1986). Interference competition has also been explored between ants and birds. For example, the presence of the red wood ant, *Formica aquilonia* Yarrow influenced *Parus major* (L.) foraging on trees (Haemig 1996). Interference competition has also been suggested between carpenter ants (*Camponotus* sp.) and spiders (Halaj *et al.* 1997), and between red wood ants (*F. rufa* group) and carabids (Hawes *et al.* 2002).

Most species of European red wood ants tend to be arboreal in their habits, foraging more intensively on foliage than on the ground (Skinner 1980, Lenoir 2003). As such there have been several studies examining the potential utility of *Formica* species as biological control agents in European forests. For example, Karhu (1998) found that as distance from *F. aquilonia* nests increased the impact of ants on defoliators decreased during the end of an autumnal moth, *Epirrita autumnata* Borkhausen (Lepidoptera: Geometridae) outbreak and during an outbreak of birch aphid, *Euceraphis punctipennis* (Zetterstedt) (Homoptera: Aphididae). A similar association was noted in mid-elevation birch (*Betula* spp.) forests during an outbreak of *E. autumnata* (Puntilla *et al.* 2004). Some species of North American red wood ants also primarily forage in trees, *e.g.*, *Formica obscuripes* Forel, a species which

may have had a significant effect on populations of defoliating insects during a spruce budworm outbreak in 1980-1992 (McIver *et al.* 1997).

Studies examining the impact of ants on epigaeic fauna are less common, and most of these examine the impact of arboreal-foraging ant species on epigaeic invertebrates. Laakso (1999) examined the soil fauna in a Finnish mixed Norway spruce (*Picea abies* (L.) Karst), silver birch (*Betula pendula* Roth) and Scots pine (*Pinus sylvestris* L.) forest, and concluded that it was unlikely that arboreal *F. aquilonia* impact epigaeic animals. Also ground-dwelling invertebrates, with the exception of Linyphiidae spiders, were not impacted when red wood ants, *F. polyctena,* were excluded from trees (Lenoir 2003). In Sweden Lenoir *et al.* (2003) suggested that *F. polyctena* is not the dominant predator of epigaeic invertebrates, likely because a large proportion of these ants forager on trees (Skinner 1980), and will increase their foraging range to access trees rather than resort to foraging on the ground (Lenoir 2003). The impact of aggressive *Formica rufa*-group ants vary within forest fragments in Finland. Of five aggressive territorial species, *F. aquilonia, F. polyctena, F. lugubris* Zetterstedt, *F. rufa* (L.), and *F. pratensis* Retzius, only *F. aquilonia* exerted a consistent impact on epigaeic invertebrates over the sampled area (Savolainen *et al.* 1989), and the other species had low impact based on their lower activity-abundances and uneven occurrence (Savolainen *et al.* 1989), assuming that encounters with ant foragers drive other ground-dwelling invertebrates out of the area.

Studies examining carabid activity-abundance and distribution have, in cases where red wood ants have been examined, shown negative associations between ant presence and carabid beetle activity-abundance (see Niemelä *et al.* 1992, Oliver and Beattie 1996, Karhu 1998, Laakso and Setala 1998, Koivula *et al.* 1999, Laakso and Setala 2000, Hawes *et al.*

2002, Koivula 2002, Foord *et al.* 2003, Koivula and Niemelä 2003, Mody and Linsenmair 2004 (*Camponotus* species), Punttila *et al.* 2004, Reznikova and Dorosheva 2004). An experimental study by Reznikova and Dorosheva (2004) indicated that carabid responses to red wood ants are species-specific. Activity-abundance of carabids of different sizes was affected to differing degrees by red wood ant presence and density (Hawes *et al.* 2002). The least affected carabids were the diurnally active *Notiophilus biguttatus* (F.) (Niemelä *et al.* 1992, Hawes *et al.* 2002). The effect of wood ant presence on carabids may be sex-specific within a species as well; Hawes *et al.* (2002) found a stronger negative correlation between red wood ant densities and female *Abax parallelepipedus* Piller & Mitterpacher than with males of the same species.

Ant nest removal experiments have resulted in the increase in biomass of predatory invertebrate mesofauna (predatory invertebrates other than ants) in Finland, this increase indicates the presence of a nearby source populations (Laakso and Setala 1998, 2000). Since thatch-mound-building ant species in Europe use foraging trail systems that are closely followed, areas exist between foraging trails that are patrolled by relatively few territorial ants (Skinner 1980, Hölldober and Wilson 1990). Areas of low or high ant density may contain low numbers of predatory invertebrate mesofauna suppressed by the ant colony. Removal of the colony may result in release from competition which allows suppressed predatory invertebrate mesofauna to increase in numbers, as observed by Laakso and Setala (1998, 2000).

Knowledge pertaining to ant ecology and distribution in British Columbia (B.C.), and in Canada in general, is sparse (Jurgensen *et al.* 2005). In particular, there is very little information pertaining to ant ecology and behaviour in northern B.C. Naumann *et al.* (1999)

summarized what is known about ants in B.C. Lindgren and MacIsaac (2002) studied the importance of dead wood as a nest substrate for forest ants in the central interior of B.C. The dominant ant that occurs in regenerating stands of 8-30 years post-harvest in west central B.C. is almost exclusively *Formica aserva* Forel (= *F. subnuda* Emery; Higgins and Lindgren in prep). *Formica aserva* is a polygynous species in the *F. sanguinea* group (Savolainen and Deslippe 1996, Savolainen and Deslippe 2001). Ants in this group are facultative slave-making ants that lack morphological specialization for the acquisition of slaves, instead relying on aggression to overwhelm other *Formica* colonies and capture pupae, a portion of which become slaves (Savolainen and Deslippe 1996). *Formica aserva* colonies produce sexual offspring later in the spring than red wood ants. Production of the sexual caste requires large amounts of protein-rich food, which *F. aserva* foragers and their slaves procure in the form of insect prey (Savolainen and Deslippe 1996).

Like the red wood ants (*F. rufa* group), *F. aserva* is aggressive and tends to occupy coarse woody debris in states of moderate decay (Lindgren and MacIsaac 2002). It probably competes with carabids for resources in habitats where they occur together. Colonies of *F. aserva* are generally patchy in distribution, but can be locally abundant with high colony densities (Francoeur 1997).

The objective of this study is to examine the effect that introduced colonies of *F. aserva* have on the carabid assemblage in young regenerating forests.

Methods

Site Selection

The site was selected based on the following criteria: absence of *F. aserva*, sufficient size to contain 40 experimental trials and a post regeneration age of 2-4 years. The study site

was located in the south Nadina, Houston Forest Products West Fraser (HFP) cutblock number 045-1. Information obtained from HFP in 2005 indicated that the block was sub boreal spruce moist cold variant (SBS mc2) with pine leading prior to harvest sub boreal spruce stands are typified by a shrub/herb layer dominated by *Cornus canadensis* L., *Vaccinium membranaceum* Dougl. ex Torr., *Lonicera involucrata* (Richards.), *Viburnum edule* (Michx.) Raf., *Rubus pedatus* Sm., *Petasites frigidus* var. *palmatus* (Ait.) Cronq., and the mosses *Ptillium crista-castrensis* (Hedw.) De Not., *Pleurozium schreberi* (Brid.) Mitt. and *Hylocomium splendens* (Hedw.) Schimp. (Meidinger and Pojar 1991).

***Formica aserva* colony selection**

Colonies of *F. aserva* in pieces of coarse woody debris (CWD) with a maximum length of 2 m and diameters between 20 cm and 40 cm were located in clearcuts between 10 and 20 years post-harvest. All colonies were collected within 50 km of the experimental plot. Colony vigour was assessed by response to disturbance; only vigorous colonies, *i.e.*, colonies that respond to disturbance with greater than 25 workers, were selected. Selected individual colonies, in CWD, were placed into body bags. Body bags prevented loss of individuals and nest material in transit. Colony selection and transport to the experimental site was undertaken on 3-9 June 2006. Colonies and their nesting substrate (CWD) were moved by truck to the study area, carried to the randomly assigned treatment replicate, and placed perpendicular to the pitfall transect.

Experimental Design and Data Collection

Ten replicates of the control and coarse woody debris treatment, and 19 ant treatments were established in a randomized complete block design. UTM coordinates for

each replicate are given in Appendix IV. Plots were separated by a linear distance of 100m from edges and neighbouring plots as determined by GPS positioning.

The control and treatments were:

1) Control - CTRL - (10 replicates) - No coarse woody debris or ants added.

2) Coarse woody debris - CWD - (10 replicates) - Single pieces of class 3 CWD, free of ants and approximately 2 m long with a diameter between 10 and 30 cm, were placed at plot center with its long axis perpendicular to randomly selected transect bearings.

3) Colony introduction - ANT - (19 replicates) - Single piece of CWD with a maximum length of 2m and a diameter between 20 and 40 cm containing a single *F. aserva* colony was placed at plot center with its long axis perpendicular to the randomly selected transect bearing.

Linear transects consisting of 10 pitfall traps were each run perpendicular to the long axis of the CWD at plot center. Pitfall traps were a modified Nordlander type after Lemieux and Lindgren (1999). Each trap was constructed out of an 8oz translucent multipurpose container (VWR catalogue number 4333-002) with a diameter of 8cm and depth of 7.5cm. Fourteen 12mm long × 6mm high entrance holes were punched below the lid of the container using a hole punch. Traps contained 90mL of 25% propylene glycol solution. Collection of samples occurred every two weeks from June 30, 2006 to September 7, 2006.

At all plots, a transect bearing was randomly selected. The treatment (CWD, ANT) or control (CTRL) was located at the transect midpoint. Pitfall traps were placed along the

transect at 0.5m, 5m, 10m, 15m and 20m in both directions (Figure 13) for a total of 10 traps per treatment plot.

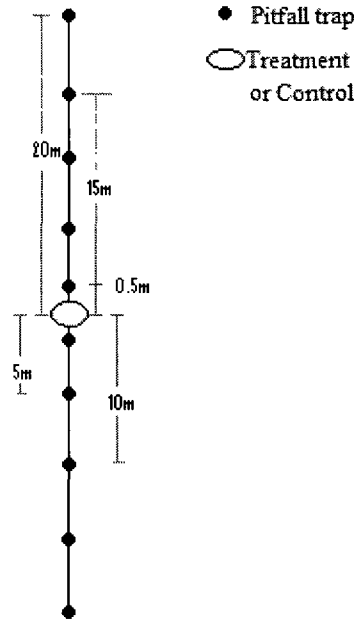

Figure 13: Diagram of trap layout for all treatment types. Closed dots indicate pitfall locations and the open dot indicates control or treatment.

A total of 390 pitfall traps were installed over 3 days, from May 31st, 2006 to June 2nd, 2006. All control and CWD replicates were started on June 2nd and 3rd, 2006, whereas the ant treatments were started on the dates that the colony was added as described above.

Data Analyses

Carabids were identified according to Lindroth (1961-1969) and sexed. Confirmation of species identification was undertaken at the Canadian Forest Service, Northern Forestry Centre, and the Strickland Entomological Museum, University of Alberta, both in Edmonton, Alberta. *Formica aserva* was identified using Wheeler and Wheeler (1963, 1986) and

Naumann *et al.* (1999). As some traps were occasionally disturbed or destroyed during a trapping period all catches were standardized by dividing the total seasonal catch by the total number of trapping days that the trap was active. Catches for within plot traps at equivalent distances were summed. The standardized catch per trap day was then multiplied by 96 to give a value representing the experimental trapping season.

A repeated measures ANOVA (SYSTAT 11, SYSTAT Software, Inc., Richmond, CA), with carabid activity-abundance as the dependent variable over trap distance from plot center as the independent variable, was used to examine the effect of trap distance from treatment center and treatment type on carabid activity-abundance. Pooled carabid data for all species were $\log_{10}+1$ transformed prior to analysis to achieve normal distribution. Data for species that comprised at less than 1 % of the total tended to be very nonnormal and had zero values for most traps, making the data unsuitable for transformation; these data, and data for the large-bodied species are graphically displayed but not statistically analysed. Species were pooled according to mean body lengths into 3 categories (Table 4) (as per Hawes *et al.* 2002). Data were then transformed to achieve a more normal distribution prior to analysis of variance. As *Trechus chalybeus* Dejean contributed nearly all the data pertaining to small species, analysis of this species can be considered the small species category. *Formica aserva* data for the ANT treatment were log transformed prior to analysis (there were no *F. aserva* in the CWD and CTRL).

Results

Of the 19 colonies of *F. aserva* relocated to randomly selected treatment plots, eight were abandoned in the first trapping period and three more by the end of the field season. In addition three colonies relocated themselves to other pieces of CWD and one colony was

consumed by a bear. Thus, a total of 11 colonies, representing 58% of those introduced, failed and were not used in the analyses. The relocated colonies and the colony that was destroyed by a bear were included, however. Samples collected during sample periods when the relocated colonies moved were discarded as it is likely that during the period of relocation the influence of the ants differed from that of established colonies. Consequently, the ANT treatments were highly variable in total sampling time varying from a low of 21 trap days to a high of 96 trap days. Control and CWD treatments were all sampled for 96 trap days. The total raw catch consisted of 25 species and 3716 specimens of carabids (Table 6).

Table 4: Carabid species collected and percent contribution by each species to the total catch. Bold indicates the most abundant species, which were analyzed individually.

Species	Individuals	Percent of catch
Trachypachus holmbergi Mannerheim‡‡	6	0.161464
Carabus taedatus Fabricius ‡	16	0.430571
Scaphinotus marginatus (Fischer von Waldheim) ‡‡	101	2.717976
Scaphinotus angusticollis Mannerheim ‡	25	0.672766
Patrobus fossifrons (Eschscholtz) ‡‡	5	0.134553
Trechus chalybeus Dejean ‡‡‡	168	4.52099
Pterostichus castaneus (Dejean)‡‡	6	0.161464
Pterostichus adstrictus Eschscholtz‡‡	691	18.59526
Pterostichus riparius Dejean‡‡	403	10.84499
Pterostichus brevicornis (Kirby) ‡‡	2	0.053821
Calathus ingratus Dejean ‡‡	32	0.861141
Calathus advena Leconte‡‡	90	2.421959
Synuchus impunctatus Say‡‡	2029	54.60172
Agonum gratiosum (Mannerheim) ‡‡	1	0.026911
Agonum cupreum Dejean ‡‡	1	0.026911
Bembidion grapii Gyllenhal ‡‡‡	5	0.134553
Amara hyperborea Dejean ‡‡	1	0.026911
Amara sinuosa (Casey) ‡‡	8	0.215285
Amara errata Kirby ‡‡	36	0.968784
Harpalus animosus Casey ‡	35	0.941873
Harpalus somnulentus Dejean ‡‡	32	0.861141
Trichocellus cognatus (Gyllenhal) ‡‡‡	2	0.053821
Bradycellus conformis Fall ‡‡‡	5	0.134553
Lebia moesta Leconte ‡‡‡	2	0.053821
Cymindis cribicollis Dejean ‡‡	6	0.161464
Unknown Carabidae*	8	0.215285
Total	3716	100

*** damaged specimens**
‡ = Large carabid group; species with a mean length > 13mm
‡‡ = Medium carabid group; species with a mean length between 6mm and 13mm
‡‡‡ = Small carabid group; species with a mean length < 6mm

A large proportion of the catch consisted of three species of carabids: 2029 *Synuchus impunctatus* Say (54.6% of the catch), 691 *Pterostichus adstrictus* Eschscholtz (18.6%), and 403 *Pterostichus riparius* Dejean (10.8%). While not significant ($F_{(2,24)} = 1.3$; $P = 0.288$), mean activity-abundances of carabids (Figure 14) were consistently higher for the ANT

treatment than for the CWD treatment and CTRL at all trap distances except at 0.5m. *Formica aserva* activity-abundance was significantly affected by distance from treatment center ($F_{(4,96)} = 10.626$; $P < 0.0001$) (Figure 15).

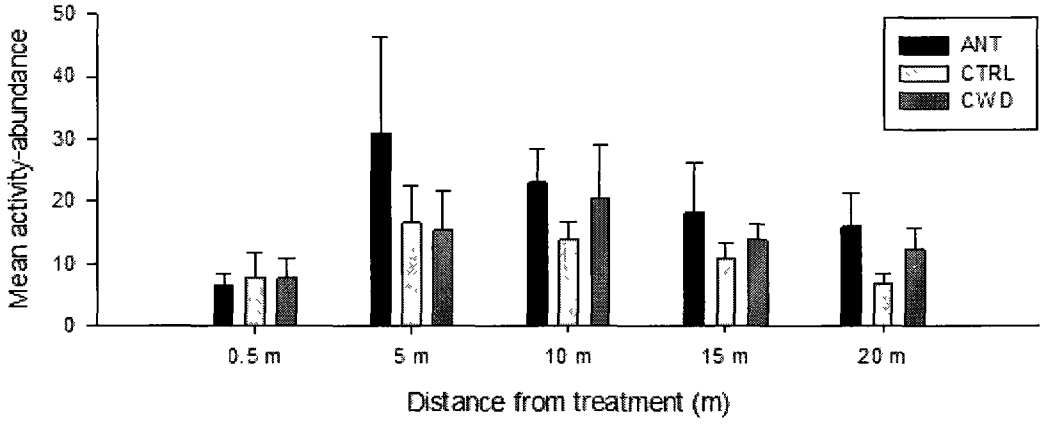

Figure 14: Pooled mean (± SEM) activity-abundances of carabids for: control (CTRL), and two treatments coarse woody debris (CWD) and *Formica aserva* nest (ANT).

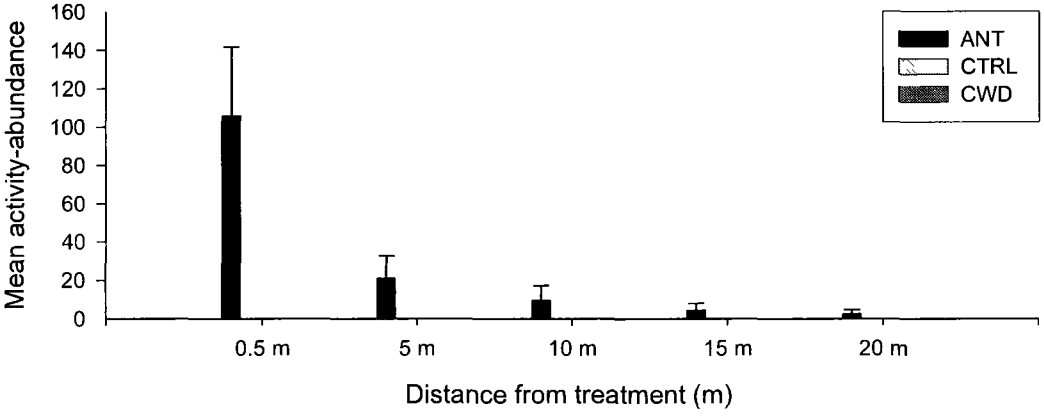

Figure 15: Mean (± SEM) activity-abundance of *Formica aserva* for: control (CTRL), and two treatments coarse woody debris (CWD) and *F. aserva* nest (ANT).

ANOVA indicated a significant effect of distance from the plot center on the mean carabid activity-abundance ($F_{(4, 24)} = 10.6$; $P < 0.001$), and no significant effect of treatment or treatment x distance.

Activity-abundance data pertaining to individual species, as well as carabids in the small, medium and large size categories did not meet the assumptions required for statistical analysis; therefore the following data summaries are descriptive rather than statistical in nature. High activity-abundance variation within species and between treatments and control, and a lack of obvious or unifying trends contribute to the inability to draw conclusions, however, activity-abundance at the 0.5m distance for all treatments was low, except for *T. chalybeus* (Figure 16). Variation in activity-abundance at other sampling distances cannot be explained by the data collected in this experiment.

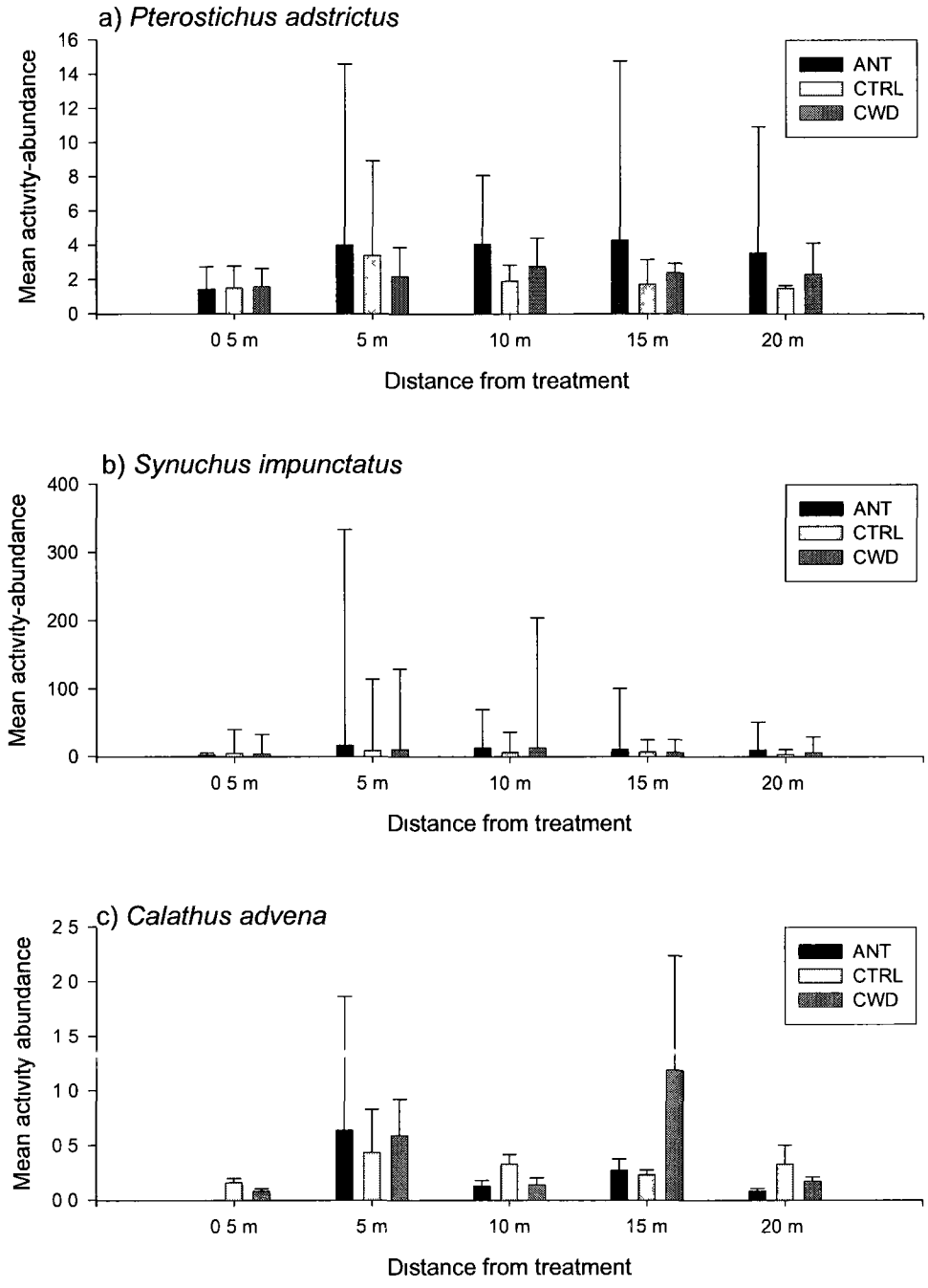

Figure 16: Mean (± SEM) activity-abundance of carabids at five distances from treatment center for control (CTRL), coarse woody debris with no ants (CWD) and coarse woody debris with a *Formica aserva* nest (ANT).

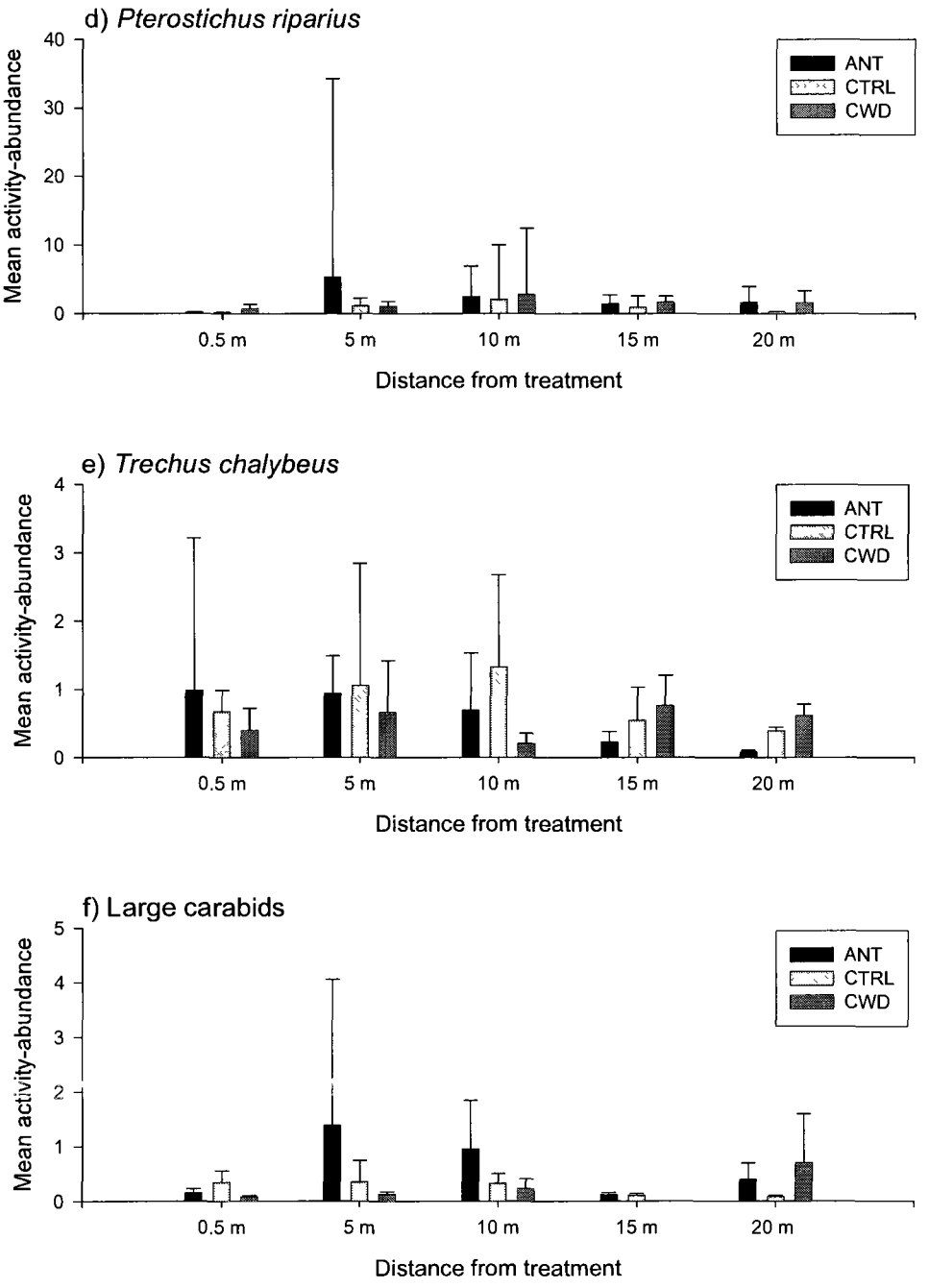

Figure 16 continued: Mean (± SEM) activity-abundance of carabids at five distances from treatment center for control (CTRL), coarse woody debris with no ants (CWD) and coarse woody debris with a *Formica aserva* nest (ANT).

Discussion

Although there was no treatment effect on the activity-abundance of the entire carabid assemblage there was a significant effect of distances from treatment center. These findings are not consistent with the findings of Reznikova and Dorosheva (2004) and Hawes *et al.* (2002) as the ANT treatment failed to show significant effects on the carabid assemblage or individual species. High variation within species and between replicates, coupled with relatively low sample sizes and non-normal data made statistical analysis for all species difficult. Species specific responses to the introduced nest were noted in shifts in activity-abundances (Figure 16), but none were significant. Depression of carabid activity-abundance at 0.5m was observed for all treatments including the control. This depression is likely due to interaction between the paired traps at 0.5m. Trap interactions and "trapping depletion" (Digweed *et al.* 1995) may have been mitigated by a different sampling protocol. Slightly higher activity-abundances of carabids at distances greater than 0.5m (with the exception of the 5m distance), for the ANT replicates when compared to control and CWD replicates, may be due to habitat differences. *F. aserva* relocate or abandon colonies when the conditions at the nest site become unfavourable (Higgins 2010). Trends observed for the control treatments (CWD and CTRL) appear to be similar for *P. adstrictus*, *S. impunctatus, T. chalybeus* and *P. riparius*. This suggests an environmental influence that more or less elicits similar responses from carabids. There is a possibility of microhabitat selection by *F. aserva* colonies, i.e., the location of a nest may be in part determined by favourable microhabitat conditions. The random assignment of treatment or control may have led to numerous nests being placed in poor habitat, leading to abandonement, which in turn may have introduced bias into the random assignment of treatment or control. Carabids are

known to have patchy distributions that infer a link to habitat quality or microhabitat availability (Niemelä *et al.* 1993). It is possible that the habitats that were good for relocated *F. aserva* colonies also happened to be good for carabids; however, higher activity-abundance of carabids 5m from *F. aserva* nests coupled with lower activity-abundances at 0.5m, suggests an interaction between carabids and *F. aserva* although trap interference is another possibility.

Observations of prey collected by foraging Formicinae suggest that carabids are a very minor prey item (Skinner 1980, Lenoir 2003). The increased activity-abundance 5m away from the nest suggest that ant colonies are excluding carabids from the area or causing carabids to alter their behaviour, *e.g*,. increasing speed of travel and reducing periods of rest (no movement), as observed for several species by Reznikova and Dorosheva (2004).

A major difficulty with introducing ant colonies for the purpose observing an effect on the resident assemblage is evenness among replicates. High variation between colonies in terms of numbers of ants and the degree of aggressive behaviour between colonies of different sizes makes interpretation difficult. The impact of colonies that have likely lost large numbers of foragers, been introduced into a novel environment, and are considerably weakened by loss of individual foragers, is probably much lower than the impact of a strong colony that has not been moved and should be considered when examining the influence ant colonies have on carabids.

Along with the results of previous research pointing to an effect by ants on carabid assemblages, my study indicates that accounting for interactions between carabids and ants may be valuable in the development and implementation of models using carabids as bioindicators. Further research into the mechanisms and species-specific behavioural

responses of carabids to ants would greatly enhance model utility and application in indicator studies

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Chapter 5: Synthesis

The purposes of my study were to: (1) describe the carabid assemblage in a cool forest ecosystem classified in the sub boreal spruce biogeoclimatic zone (Meidinger and Pojar 1991), and assess the effect of clearcut harvesting, and how carabid communities change in post-harvest stands as forest succession proceeds and stand canopies close (Chapter 2); (2) examine the effect of two abundant species of ants, *Formica aserva* Forel and *Camponotus herculeanus* (L.) on carabid activity-abundance, and injury frequency in stands with varying canopy closure (Chapter 3); and (3) measure interactions between carabids and *F. aserva* in a young regenerating stand through experimental introduction of ant nests (Chapter 4).

The theory that an organisms' environment influences its ability to exist, persist, and thrive, is a basic principle of ecology. Determining where a species exists is a prerequisite to exploring more specific questions concerning population and community ecology (Krebs 1972). In west central British Columbia, little base line data pertaining to ants and carabids and their interactions exist, but such data are essential to answer basic ecological questions. To this end, I collected data regarding the composition, and basic habitat associations of carabids within unharvested and harvested sub boreal spruce stands using a chronosequence (Chapter 2).

Thirty one species of carabids and 4801 individual specimens were continuously collected over 6 two week sampling periods from May 25, 2005 until August 28, 2005 (Chapter 2; Table 1). For the common carabid species that contributed at least 2% of the total catch, differences in seasonal activity-abundances and sex ratios were examined and found to significantly vary for *Scaphinotus marginatus* Fischer, *Scaphinotus angusticollis*

Fischer, *Pterostichus adstrictus* Eschscholtz, *Pterostichus riparius* Dejean, *Calathus advena* Leconte, *Calathus ingratus* Dejean, *Synuchus impunctatus* Say, but not for *Trechus chalybeus* Dejean (Chapter 2; Figure 2; Appendix II). For the two *Scaphinotus* species and *S. impunctatus*, the trends observed differed from those observed in other geographic locations and in differing forest type associations, suggesting that some species of carabids may be quite plastic in their habitat associations and seasonal activity patterns. It is, however, important to note that information on forest cover associations and seasonality is rare or absent from the literature for some of the species in my study, although information for several species has been summarized by Larochelle and Larivière (2003), and the University of Alberta Strickland Entomological Museum on line data base[2].

Differences in activity and broad habitat associations are likely driven by coarse-scale environmental differences that occur over large geographic areas (Work *et al.* 2008). Consideration of variability in carabid species' seasonal activity-abundance is especially important if an indicator value is placed on individual species' proportional contribution to a given assemblage. In addition, it is important to recognize that the response to an indicator value of any given species may differ depending on the ecosystem in which it is being studied, and the composition of the epigaeic community.

Many carabid studies have sought to elucidate differences in carabid assemblage composition in differing habitats across broad geographic areas encompassing several different ecosystems. This large-scale examination of variation has demonstrated different habitat associations for carabids (Atlegrim *et al.* 1997, Ings and Hartley 1999, Heyborne *et al.* 2003, Vance and Nol 2003, Brouat *et al.* 2004, de Warnaffe and Lebrun 2004), but has

[2] http://www.entomology.ualberta.ca/index.html. Accessed 2009-11-13.

not specifically examined how disturbance influences carabids within a single forest ecotype through the successional progression from clearcut to mature forest. In my study, I was able to examine shifts in carabid assemblage composition associated with succession; similar trends have also been observed in carabid communities associated with stand succession in other forest types (Baguette and Gerard 1993, Niemelä *et al.* 1993, Brumwell *et al.* 1998, Koivula *et al.* 2002, Lemieux and Lindgren 2004). Variation in carabid species composition occurred with shifts in canopy cover (analogous to time since disturbance), which is consistent with the findings of other studies (Magura and Tothmeresz 1997, Brumwell *et al.* 1998, Humphrey *et al.* 1999, Jukes *et al.* 2001, Koivula 2002, Koivula *et al.* 2002, Magura 2002, Magura *et al.* 2002, Heyborne *et al.* 2003, Lassau *et al.* 2005). Of the 21 species included in nonmetric multidimensional scaling analyses, four clusters or habitat association groups, and a single species "group", were observed (Chapter 2; Figure 4). Grouping of species tended to be governed primarily by variation contributed by positive correlations with a high grass component of ground cover and by positive correlations with canopy cover, high needle component of ground litter, and diversity in vegetation, as well as a negative correlation with slash. Forest cover alters the forest floor environment as it develops (Hamilton 1988). As the canopy increases with time since disturbance, the ability of organisms that occupy the forest floor to acquire resources change, as do the resources they utilize and their thermal environment. Niemelä *et al.* (1993) noticed higher diversity and activity-abundance of carabids in stands with developing canopies in Alberta. They attributed this to the occupation of such disturbed habitats by forest generalist species, open ground specialists that have persisted as the canopy cover has increased, and forest specialists that are beginning to re-occupy the as colonists. This pattern was not observed in

my study. Carabid diversity and activity-abundance was highest in mature stands and in stands without canopies. As canopy cover increased with time since disturbance, in keeping with general forest succession models, additional factors appeared to reduce either, the quantity of habitat available to carabids, the resources available to them, or some combination of both. This factor appears to be ants, specifically *Formica aserva*. Exactly how *F. aserva* influences the habitat or the ability of carabids to acquire resources will require additional research.

While forest canopy (Magura and Tothmeresz 1997, Brumwell *et al.* 1998, Humphrey *et al.* 1999, Jukes *et al.* 2001, Koivula 2002, Koivula *et al.* 2002, Magura 2002, Magura *et al.* 2002, Heyborne *et al.* 2003, Lassau *et al.* 2005) and vegetation (Hawes *et al.* 2002, Brose 2002, Vanbergen *et al.* 2007) influence habitat suitability for carabids, it appears that the presence of ants influences their finer scale spatial distribution (Reznikova and Dorosheva 2004). Data displaying negative associations (Chapter 3: Figure 10) shows a trend towards aversion towards *F. aserva* in most of the abundant species of carabids, with a weaker trend, that may be due to lower ant numbers, towards *C. herculeanus*. The aversion of carabids to ants, particularly *Formica rufa*-group (so called red wood) ants, has been seen in numerous carabid ecology studies (Niemelä *et al.* 1992, Oliver and Beattie 1996a, Karhu 1998, Laakso and Setala 1998, Koivula *et al.* 1999, Laakso and Setala 2000, Hawes *et al.* 2002, Koivula 2002, Foord *et al.* 2003, Koivula and Niemelä 2003, Mody and Linsenmair 2004 (*Camponotus* species), Punttila *et al.* 2004, Reznikova and Dorosheva 2004). Further analysis of the influence of *F. aserva* on carabids indicated that there is an activity-abundance threshold of *F. aserva* above which carabid activity-abundance is significantly lowered (Chapter 3: Figure 7). This trend was also suggested in the *F. aserva* colony

introduction experiment, where carabid activity-abundance was slightly higher (but not significantly so) near colonies than in control plots although trap interactions were likely a factor as well (Chapter 4: Figure 14). While this may appear to indicate that carabids increase in the presence of ants, a more likely explanation is that carabids alter their behaviour in the presence of ants as observed by Reznikova and Dorosheva (2004). By increasing rates of movement and decreasing resting periods in the presences of ants the probability of carabids getting caught in pitfall traps will increase, even if the absolute number of carabids in the proximity of a trap is no higher.

The interaction between carabids and *F. aserva* may result in detrimental effects on the carabids. While evidence of carabids as prey of ants has not been reported in the literature a significantly higher proportion of carabids tend to be injured in plots with moderate *F. aserva* activity-abundance (Chapter 3: Figure 9). As *F. aserva* colonies mature, and grow in size, it is possible that these ants shift from being an ineffective predator that interferes with carabids to an effective predator with a higher capture rate, which results in lower carabid injury frequency (Chapter 3: Figure 9). Species-specific trends in injury frequency support the assertion that in stands with *F. aserva* present, the frequency of collecting injured carabids was significantly higher than the frequency of injury in stands where *F. aserva* were absent (Chapter 3: Table 4). These stands also tended to be those with developing canopies and significantly lower carabid diversity (Chapter 2: Table 2). While the evidence indicating that *F. aserva* is responsible for injuries to carabids is circumstantial, it is nevertheless compelling (Chapter 3). Additional trials, specifically designed to investigate if similar injuries can be replicated, either in laboratory settings or the field, would be required for a definitive determination of cause and effect.

In examining the data presented in Chapter 4, one cannot help but notice the overall higher (but not significantly so) carabid activity-abundance in the ant treatment compared to the controls. While colony failure was anticipated in the experimental design (58% of the relocated colonies were unsuccessful), the possibility that within stand variation in the treatment plots would influence colony success was not. The failure of colonies tended to occur in spots that could possibly be considered poor habitat, not just for *F. aserva* but also for the carabids.

Within the sub boreal spruce stands examined, and in other habitats, carabids have been shown to be selective in their habitat choices (Niemelä and Halme 1992, Niemelä *et al.* 1992). In my study, habitat-use by differing groups of carabids (Chapter 2: Figure 4) seems to be driven by canopy cover, as well as vegetative structure and composition, although there is also an aversion to the presence of *F. aserva* in carabid assemblages (Chapter 3: Figure 8) as well as in most of the abundant species collected (Chapter 3: Figure 10). Habitat selectivity has also been demonstrated to occur in ants. Selection can be influenced by thermal requirements (Higgins in press), prey species availability; including competitive exclusion (Nonacs and Dill 1990), or nesting substrate/host species. Therefore it is possible that in the colony-introduction experiment, *F. aserva* that persisted "chose" to remain at the location where they were placed because of a favourable habitat, while the other nests relocated to more favourable sites or failed. These favoured sites may also have been higher quality habitats for the carabids. Therefore, it is likely that carabids, in the absence of *F. aserva*, would select similar if not the same habitat patches that ant colonies essentially exclude them from during stand successional stages favouring ants, as shown in the negative associations in Chapter 3 (Figure 10).

Use of similar habitats, exploitation of similar resources and co-occurrence at the same time and in the same space likely leads to interaction. The presence of a larger proportion of injured carabids, and fewer carabids leads to the conclusion that competition to the detriment of carabids occurs where *F. aserva* and individual carabids come into contact, and predation is a possible outcome when *F. aserva* activity is high.

Use of species or species groups as indicators of various environmental conditions or to observe the effects of management on ecosystems has proceeded as a cost and time effective technique to observe a variety of effects (Weaver 1995, Rainio and Niemelä 2000, Maleque *et al.* 2006, Work *et al.* 2008). An issue with indicator species has been interpretation of observed responses. Are the indicator organisms responding to the environmental condition in question (Dale and Beyeler 2001), *e.g.*, forest health condition, coarse woody debris, habitat fragmentation *etc.*, or are they being influenced by unknown variables? While carabids have be shown to be useful as indicators (Rainio and Niemelä 2000, Work *et al.* 2008), the need for understanding the influences and interactions that occur within the broader epigaeic invertebrate community has been demonstrated by my study. The negative association with ants has been noted in several studies, and confirmed in this study. This relationship has, however, been under-acknowledged in carabid studies (Lövei and Sunderland 1996) and is a potentially major influencing factor of carabid activity-abundance. The level of influence exerted by ants may influence the interpretation of findings where carabids are used as indicators, particularly when aggressive ant species are abundant.

In examining the interaction between carabids, and the ants *F. aserva* and *C. herculeanus*, I have provided compelling evidence that single taxon studies examining

invertebrate epigaeic community ecology should be re-examined, as they only paint a partial picture of the community as a whole. Broadening the scope of invertebrate species examined in community ecology is not a novel idea, as research into the feasibility of using recognizable taxonomic units, or morphospecies, for rapid assessment of invertebrate diversity have been tested in many areas, e.g., Australia (Oliver and Beattie 1996b) and New Zealand (Derraik *et al.* 2002). While use of the morphospecies concept should not be viewed as a replacement for species level taxonomic expertise, it may be useful for accounting for the diversity in forest arthropod communities and may provide a great deal of initial information pertaining to the interactions therein.

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Appendices

Appendix I
Study Site Locations 2005

1) Non-harvested plots (n=2).
Site One: Tanglechain (Houston Forest Products)
Nearest road access at UTM 09U 658641E 6092206N. This is not far off of the Tanglechain road near the beginning of the NSR cutblock 428.
0,0 of plot is 9U 620813E 5984110N

2) Post-harvest sites (2 years) n=2.
Site One: Chisholm (Houston Forest Products)
Cutblock number 631-TH2
09U 613828E 6007491N
Site Two: Nadina South (Houston Forest Products)
Cutblock number 045-1
09U 630054E 5969832N
Elevation 1018m

2) Post-harvest sites (8-10 years) n=2.
These sites were adjacent to the mature sites under 1 above
Site One: Tanglechain (Houston Forest Products)
Cutblock number 452-2 09U 0664241 6087541N
Site Two: Nadina West (Houston Forest Products)
Cutblock number 021-1
09U 621437E 5984074N

3) Post-harvest sites (14-18 years) n=2.
Site One: Nadina West 15 (NW15): Block 011-1
-off Duel Lake Road
09U 0623613E 5982200N
Elevation 1051 m
Site Two: Tanglechain (Houston Forest Products)
Cutblock number 451-2
09U 669405E 6089080N

4) Post-harvest sites (>25 years) n=2
Site One: Pimpernel 25 (P25):
Immediately to the north of block 342-110
09U 0630078E 6003705N
Elevation 875m
Site Two: Morice River (MR25):
-along Morice river road just after 48 km
09U 06223826E 6002697N
Elevation 816m

Appendix II

ANOVA Results Figure 2 Chapter 2

ANOVA results for variation in activity-abundance for the sexes and over sample periods, seasonal effect. *P*-value indicates significant variation in activity-abundance between sexes and over sample periods ($\alpha = 0.05$).

Gender	SS	df	MS	*F*	*P*
Scaphinotus marginatus	74.1	4	18.53	7.71	0.000
Error	17.89	745	2.4		
Scaphinotus angusticollis	33.4	4	8.35	5.25	0.000
Error	11.86	745	1.59		
Pterostichus adstrictus	16.38	4	4.09	3.35	0.010
Error	911.37	745	1.22		
Pterostichus riparius	5.94	4	1.48	3.97	0.003
Error	278.86	745	0.37		
Calathus advena	132.7	4	33.18	17.85	0.000
Error	1384.57	745	1.86		
Calathus ingratus	2.07	4	0.52	6.28	0.000
Error	61.44	745	0.08		
Synuchus impunctatus	186.45	4	46.61	9.15	0.000
Error	3796.29	745	5.09		
Season					
Scaphinotus marginatus	18.9	4	4.72	8.19	0.000
Error	430.54	745	0.58		
Scaphinotus angusticollis	14.1	4	3.53	7.5	0.000
Error	350.5	745	0.47		
Pterostichus adstrictus	6.27	4	1.57	4.3	0.002
Error	271.75	745	0.37		
Pterostichus riparius	0.82	4	0.66	1.19	0.312
Error	128.27	745	0.84		
Calathus advena	5.69	4	1.42	2.88	0.022
Error	367.72	745	0.49		
Calathus ingratus	0.57	4	0.14	3	0.018
Error	35.29	745	0.047		
Synuchus impunctatus	3.99	4	1	1.32	0.262
Error	564.49	745	0.76		

F- Test analysis of the influence of seasonal variation on abundant male and female carabid activity-abundance. *P*-value indicates a significant effect of season on the mean activity-abundance of either male or female carabids ($\alpha = 0.025$)

	SS	df	MS	*F*	*P*
Female *Scaphinotus marginatus*	12.34	4	3.09	3.21	0.012
Error	715.25	745	0.96		
Male *Scaphinotus marginatus*	80.66	4	20.16	9.99	0.000
Error	1504.41	745	2.01		
Female *Scaphinotus angusticollis*	3.55	4	0.89	1.08	0.362
Error	609.62	745	0.82		
Male *Scaphinotus angusticollis*	43.94	4	10.99	8.83	0.000
Error	926.51	745	1.24		
Female *Pterostichus adstrictus*	17.41	4	4.35	4.35	0.002
Error	744.51	745	1		
Male *Pterostichus adstrictus*	5.25	4	1.31	2.23	0.065
Error	438.81	745	0.59		
Female *Pterostichus riparius*	5.29	4	1.32	3.53	0.007
Error	278.77	745	0.37		
Male *Pterostichus riparius*	1.47	4	0.37	2.14	0.074
Error	128.36	745	0.17		
Female *Calathus advena*	96.37	4	24.09	13.42	0.000
Error	133.74	745	1.8		
Male *Calathus advena*	42.03	4	10.51	18.86	0.000
Error	41.49	745	0.56		
Female *Calathus ingratus*	2.34	4	0.58	6.1	0.000
Error	71.46	745	0.1		
Male *Calathus ingratus*	0.3	4	0.08	2.22	0.065
Error	25.27	745	0.03		
Female *Synuchus impunctatus*	106.34	4	26.58	10.08	0.000
Error	1964.57	745	2.64		
Male *Synuchus impunctatus*	84.1	4	21.01	6.54	0.000
Error	2396.2	745	3.22		

Appendix III
Non metric Multidimensional Scaling: PC – Ord Outputs

Coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space:

	R^2	
Axis	Increment	Cumulative
X	.188	.188
	.170	.358
Y	.370	.728

Increment and cumulative R-squared were adjusted for any lack of orthogonality of axes.

Axis pair	r	Orthogonality,% = 100(1- r^2)
X vs Y	-0.201	96.0

Number of entities = 150
Number of entity pairs used in correlation = 11175
Distance measure for ORIGINAL distance: Sorensen (Bray-Curtis)

Final Stress = 20.34
Final instability = 0.00569

Pearson Kendall Species Correlations with NMS axes: Chapter 2 Figure 4

Axis:	X			Y		
	R	R^2	tau	*R*	R^2	tau
Variables						
NOTSYL	0.069	0.005	0.078	0.122	0.015	0.083
SCAMAR	0.131	0.017	0.114	0.624	0.389	0.61
SCAANG	-0.103	0.011	-0.177	0.706	0.498	0.686
PTEADS	0.118	0.014	0.076	-0.468	0.219	-0.396
PTEBRE	-0.092	0.008	-0.11	0.061	0.004	0.038
CALADV	-0.153	0.023	-0.245	0.449	0.201	0.488
CALING	-0.092	0.008	-0.023	0.18	0.032	0.185
SYNIMP	0.653	0.426	0.636	-0.293	0.086	-0.364
AMASIN	0.05	0.003	0.036	-0.206	0.042	-0.232
AMAERR	0.351	0.123	0.272	-0.284	0.081	-0.297
HARSOM	0.072	0.005	0.027	-0.358	0.128	-0.299
TRECHA	0.432	0.187	0.252	-0.183	0.033	-0.233
BEMGRA	-0.008	0	-0.018	-0.244	0.06	-0.196
PTECAS	-0.159	0.025	-0.152	0.049	0.002	0.046
BEMFOR	0.267	0.071	0.211	-0.13	0.017	-0.105
PTERIP	0.248	0.061	0.176	-0.061	0.004	-0.118
ELALAP	0.282	0.08	0.316	-0.173	0.03	-0.178
AGOAFF	0.131	0.017	0.14	-0.116	0.013	-0.115
BRACON	0.238	0.057	0.218	-0.149	0.022	-0.12
STEHAE	-0.184	0.034	-0.179	0.219	0.048	0.185
LEBMOE	-0.025	0.001	-0.08	-0.197	0.039	-0.188

Pearson and Kendall Variable Correlations: Chapter 2 Figure 4

Axis:	X			Y		
	R	R^2	tau	*R*	R^2	tau
Variables						
CCOVER	-0.394	0.156	-0.27	0.838	**0.702**	0.569
LCOVER	-0.102	0.01	-0.066	0.074	0.005	0.024
HCOVER	-0.365	0.133	-0.233	0.22	0.048	0.175
CWD	-0.166	0.028	-0.119	0.052	0.003	0.028
MOSS	-0.397	0.158	-0.314	0.374	0.14	0.275
SLASH	0.031	0.001	0.11	-0.553	**0.305**	-0.465
GRASS	0.486	**0.237**	0.398	-0.335	0.112	-0.26
BAREGR	0.022	0	0.036	-0.278	0.077	-0.254
REDROT	0.212	0.045	0.178	-0.026	0.001	-0.036
NEEDLE	-0.066	0.004	-0.064	0.569	**0.324**	0.474
LITTER	0.088	0.008	0.089	-0.019	0	-0.017
LINBOR	0.074	0.005	0.089	0.052	0.003	-0.014
VEGDEN	0.238	0.056	0.127	0.001	0	-0.026
VEGDIV	-0.044	0.002	-0.047	0.502	**0.252**	0.329
COVDIV	-0.012	0	0.016	-0.115	0.013	-0.079

Appendix IV

UTM's For Experimental Replicates Chapter 4

Replicate	Treatment	UTM	Replicate	Treatment	UTM
1	ANT	09 629105E 5968708N	21	CWD	09 629091E 5968806N
2	CWD	09 629216E 5968722N	22	ANT	09 629008E 5968735N
3	CTRL	09 629270E 5968796N	23	CTRL	09 630264E 5970275N
4	ANT	09 629294E 5968895N	24	ANT	09 630212E 5970189N
5	ANT	09 629362E 5968865N	25	CWD	09 630157E 5970104N
6	ANT	09 628493E 5968808N	26	ANT	09 630060E 5970084N
7	CWD	09 628577E 5968861N	27	CTRL	09 629962E 5970109N
8	CTRL	09 628644E 5968936N	28	CWD	09 630047E 5970185N
9	CTRL	09 628713E 5969014N	29	CWD	09 630126E 5970246N
10	ANT	09 628791E 5969079N	30	ANT	09 630188E 5970321N
11	ANT	09 628678E 5969139N	31	ANT	09 630247E 5970442N
12	ANT	09 628617E 5969031N	32	CTRL	09 630140E 5970419N
13	CWD	09 628551E 5968957N	33	CWD	09 630064E 5970347N
14	ANT	09 628462E 5968901N	34	ANT	09 629975E 5970301N
15	CWD	09 628395E 5968822N	35	ANT	09 629848E 5969635N
16	ANT	09 628305E 5968872N	36	CTRL	09 629817E 5969731N
17	CTRL	09 628377E 5968942N	37	ANT	09 629819E 5969836N
18	CWD	09 628483E 5968997N	38	ANT	09 630010E 5969836N
19	CWD	09 628536E 5969084N	39	ANT	09 630015E 5969730N
20	ANT	09 629178E 5968861N	40	CTRL	09 630117E 5969744N